Response of benthic invertebrate fauna to fluctuating lake levels and salinity concentrations in Lake Ellesmere/Te Waihora

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Abstract

Lake Ellesmere/Te Waihora is one of New Zealand's largest coastal, brackish water lakes. It has nationally significant wetland bird populations and is regionally important for iwi. The lake regularly experiences fluctuations in water level, resulting in a continually expanding and contracting littoral zone. This study investigated the impacts of these water level changes on the ecology of the lake. Water chemistry results collected over 12 months, confirm the lake is hypertrophic, due to high nutrient (nitrogen and phosphorus) concentrations resulting in high chlorophyll *a* levels and low water clarity. Water chemistry conditions were collected at five locations around the lake and showed marked spatial variation, with the eastern most end (Kaituna Lagoon) having generally the best water quality and lowest salinity (mean 4.9 ppt). Mean concentrations of total nitrogen ranged from 1.63 to 2.4 mg/L, chlorophyll *a* from 50 to 148 *u*g/L and total suspended solids from 151 – 248 mg/L. Seasonally, highest nutrient concentrations (mean, total nitrogen = 2.625 mg/L, dissolved reactive phosphorus = 0.059 mg/L and total phosphorus = 0.365 mg/L) occurred in late summer months (February – March), slightly decreasing but remaining high throughout winter.

The benthic invertebrate community was surprisingly diverse, Crustacea (*Paracorophium excavatum*), Oligochaeta, Mollusca (*Potamopyrgus antipodarum*) and Chironomidae (*Chironomus zealandicus*) were dominant community members in the littoral zone, although 24 other taxa were collected. At high water levels, taxonomic richness increased in the eulittoral zone, while decreasing in the mid-littoral and lower littoral zones. In contrast, density decreased with higher water level in the eulittoral and mid-littoral zones, while increasing in the lower littoral zone. Benthic invertebrate communities appeared to be adapted to periods of intermittent dewatering, and even sustained dewatering under cooler temperatures. Despite the relatively high diversity of benthic invertebrates, invertebrate predators are generally absent from the lake. My results suggest multiple factors and interactions from predation pressure, salinity and lack of macrophytes are likely responsible for the absence of predatory invertebrates such as damselfly (*Xanthocnemis zealandica*) and dragonfly (*Procordulia grayi*) larvae.

The lack of significant relationships between water quality variables and water level, and the positive relationship between chlorophyll *a* and salinity, suggests that current lake opening events do not have a positive effective on either water quality or phytoplankton biomass in

Lake Ellesmere/Te Waihora. However, the current lake opening regime seems to be favourable to benthic invertebrate survival in the littoral zone, as the lake is predominantly open over winter when temperatures are lower, reducing the risk of desiccation. Anthropogenic activities which modify hydrodynamic and water quality conditions can potentially have a large negative impact on the structure and diversity of the littoral invertebrate community as well as flow on effects through the lake food web. Based on results from this study, I suggest a minimum lake level at Taumutu of 0.6 m during the months from November – April in order to protect benthic invertebrate communities in the eulittoral zone from extensive loss of habitat, extreme temperature and reduced risk of desiccation. Having a minimum set at ~0.6 m would provide sufficient littoral zone habitat for the lakes extensive bird life and fish populations. In addition, immediate efforts are needed into reducing nutrient loads into the lake, through improved farm management (nutrient and stocking budgets) and riparian fencing. Furthermore, physical and chemical water quality properties would benefit from an increased water level over summer months, by reducing water temperatures, diluting readily available nutrient concentrations and potentially reducing phytoplankton (and potentially toxic cyanobacterial) blooms.

Chapter 1

Introduction
Lake Ellesmere/Te Waihora

1.1 Introduction

Shallow lowland lakes and coastal lagoons are under increasing threat from anthropogenic activity, owing to their location at the lower reaches of their catchments where they act as a sink for contaminants from upstream. Despite the obvious trend for declining lowland lake health (Drake *et al.,* 2009), most limnological research has focused on deeper alpine lakes (Reid 2005; Hamill 2006). Lake Ellesmere/Te Waihora is a large (20 000 ha), shallow, brackish lake, southwest of Banks Peninsula, in Canterbury, New Zealand (Figure 1.1). The lake contains a significant proportion of Canterbury's aquatic and terrestrial biodiversity (Taylor 1996), was historically a major eel and flounder fishery, retains important cultural and recreational values and is recognised as one of New Zealand's most important wetland systems for its outstanding wildlife (Taylor 1996; Hughey & Taylor 2009). However, over the last few decades, Lake Ellesmere/Te Waihora has exhibited evidence of declining water quality (Hughes 1974; Taylor 1996), a hyper-trophic status (Hayward & Ward 2006) and declining extant recreational, commercial and customary fisheries (Jellyman & Chisnall 1999; Jellyman & Smith 2009). This decline in water quality has primarily been attributed to cumulative effects of decades of intensifying agricultural activity in the lakes catchment and subsequent nutrient runoff into tributary streams (Hayward & Ward 2006; Wood 2008; Schallenberg *et al.,* 2010). Currently, the lake experiences several compounding management issues in addition to nutrient enrichment; artificial lake level management, commercial fish harvesting, cumulative impacts from water abstraction from inflowing groundwater and streams, and the effects of invasive pests (e.g., Willows; Pompei & Grove 2009). Lake level management is believed to be of particular significance due to alterations in the natural salinity regime that have occurred as a consequence.

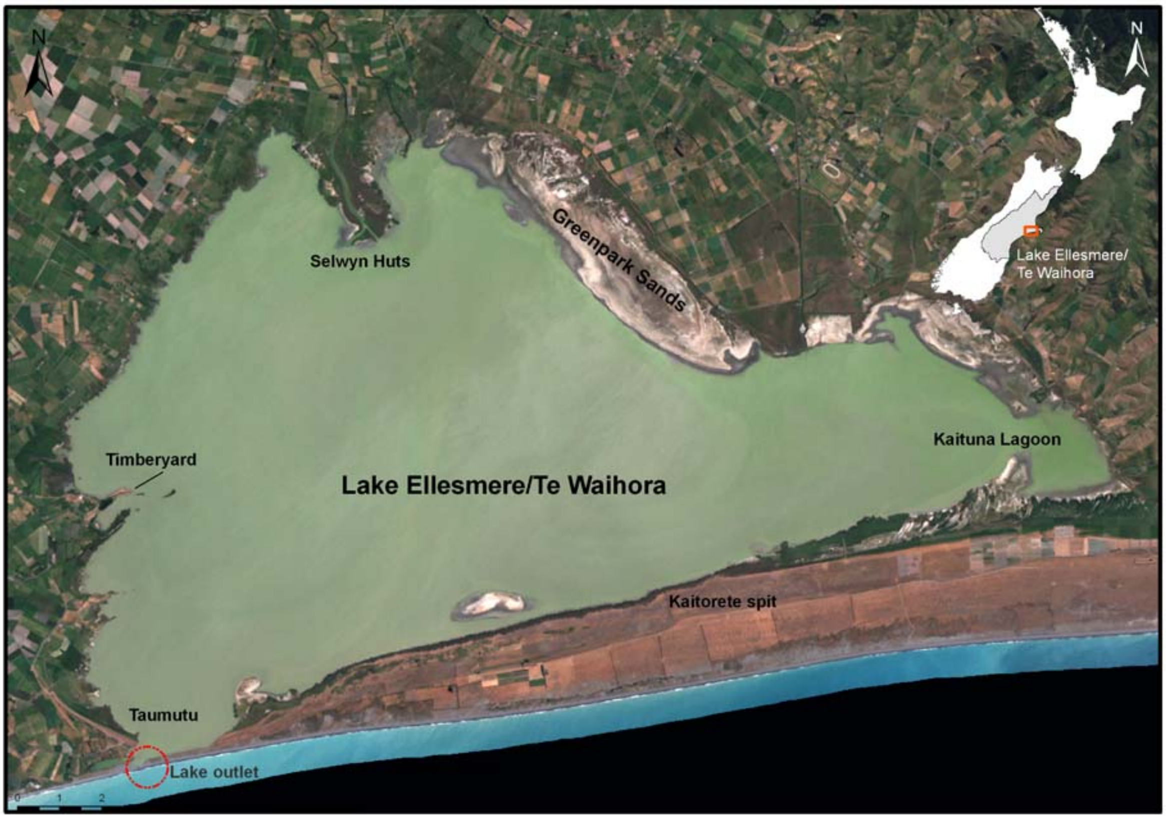


Figure 1.1 Lake Ellesmere/Te Waihora, Canterbury, New Zealand.

1.1.1 Lake Ellesmere/Te Waihora

Lake Ellesmere/Te Waihora is a complex system that has undergone many transformations since its formation nearly 3000 years ago; from a major discharge point for the Waimakariri River, tidal estuary, freshwater lake and today a brackish lake (Hughes *et al*., 1974; Kirk 1994; Gerbeaux & Ward 1991; Taylor 1996). The most recent major change in lake state occurred after the Wahine storm in April 1968, during which the lake switched from a clear macrophyte dominated system to a turbid phytoplankton dominated state. Prior to this event, macrophytes are believed to have acted as a buffer against wave action so that the littoral zone of the lake had high water clarity. However, the mid-lake would have still have exhibited a moderate degree of turbidity, especially during and after windy periods (Schallenberg *et al.,* 2010). There were reports of periods prior to the Waihine storm where macrophytes died-off, but were able to re-establish themselves (Hughes *et al*., 1974). After the Waihine storm however, macrophytes were unable to re-establish. This change in state has been attributed primarily to hurricane force winds that devastated the beds of *Ruppia* *megacarpa* and *Potamogeton pectinatus,* subsequently destabilising bottom sediments (Hughes *et al*., 1974).

Wind and wave action have since maintained the high suspension of bottom sediment, reducing water clarity and light penetration and limiting re-establishment of macrophytes (Sager *et al*., 2004; Jellyman *et al*., 2009). This change in state has almost certainly had major effects on the ecology of the lake, although there is paucity documentation. The previously abundant black swan (*Cygnus atratus*) population underwent a four-fold decrease in the 5 years after the Wahine storm due to a reduction in macrophyte beds, their primary food resource (Williams 1979; Hamilton 1990; McKinnon & Mitchell 1994; Sagar *et al*., 1995). Comparisons of current research on food web structure with available historical data also suggest a shift in the benthic invertebrate community. Where previously dominated by *Potamopyrgus antipodarum* (prior Wahine storm) the lake is now dominated almost entirely by *Chironomus zealandicus* and oligochaetes (Dawn 1995; Sagar *et al.,* 2004; Wood 2008; Kelly & Jellyman 2007). Furthermore, a number of recent studies have found the lake to be virtually devoid of invertebrate predators (Sagar *et al.,* 2004; Wood 2008; Kelly & Jellyman 2007), such as damselfly and dragonfly larvae, which are typically common in other New Zealand lake ecosystems (Biggs & Malthus 1982; Talbot & Ward 1987; Crumpton 1997; Rowe & Graynoth 2002). One possible explanation for the absence of invertebrate predators in Lake Ellesmere/Te Waihora is fluctuating salinity levels. Other possible factors include the lack of macrophytes (habitat and refuge), water level fluctuation (inability to withstand desiccation and frequent disturbance) and predation pressure from fish and birds.

Further research has focused on the feasibility of re-establishing macrophytes in Lake Ellesmere/Te Waihora to help improve water quality. The primary limiting factors appear to be the ready re-suspension of fine sediment in the water column resulting in high turbidity and subsequent decreased light penetration (Sagar *et al.,* 2004; Jellyman *et al.,* 2009). Fluctuating water levels (James *et al.,* 1998; James & Graynoth 2002) and salinity concentrations (Barker *et al*., 2008), have also been linked to reduced diversity, biomass and production of macrophytes in lake systems, due to their inability to cope with osmotic stress (Hammer & Heseltine 1988; Wollheim & Lovvorn 1995). In summary, although a number of studies have been conducted on aspects of the ecology of the lake (Dawn 1995; Sagar *et al.,* 2004; Kelly & Jellyman 2007; Woods 2008; Jellyman *et al.,* 2009), relatively little is known about the impacts that lake level fluctuation and salinity have on the food web in Lake Ellesmere/Te Waihora.

1.1.2 Lake opening

Historically, Lake Ellesmere/Te Waihora covered a much larger area than at present, approximately 30 000 ha, and was markedly deeper at maximum 5 m (Hughes *et al.,* 1974; Taylor 1996). Prior to anthropogenic modification the lake was opened to the sea when freshwater pressure within the lake was sufficient to breach the gravel barrier along Kaitorete spit (a.s.l ~ 4 m; Taylor 1996). It has been estimated that the lake opened naturally once every 4 years and may have remained open for a long time (> 1 year). This would have resulted in the lake becoming more estuarine in character during the open period, but also primarily freshwater during closure. Prolonged periods of closure would have had implications for fish migration and threatened to flood shoreline settlements. Anecdotally, Maori are known to have begun artificial lake openings using horse-drawn scoops (Taylor 1996). Environment Canterbury and its predecessor the North Canterbury Catchment Board have managed the lake openings since 1947 (Taylor 1996). Since then, lake openings have been manually controlled, and the pattern and duration of openings have consequently been completely altered from the natural state. This has resulted in a more brackish environment due to the increased regularity of opening events (2 – 4 times per year; Fenwick & Image 2002) and lower average lake level (~ 1 m; Kirk & Lauder 2000). Today, the lake still has no permanent outlet, and during periods of high rainfall and high lake level fringing agricultural land (14 000 ha) is highly susceptibility to flooding (Taylor 1996). Lake opening criteria are set by the Water Conservation Order (1990) and prohibits lake openings other than: when lake level exceeds 1.05 m above mean sea level (m.s.l) between 1st August and 31st March and when lake level exceeds 1.13m above m.s.l between 1st April and 31st July (Fenwick & Image 2002). When the lake meets its trigger level a group of representatives (contracted by Environment Canterbury), from Nhai Tahu, Fish and Game, Department of Conservation, ratepayers and lake-fisherman, decide whether the lake should be opened under the terms of the five year consent (Butcher 2009). Typically the lake is opened by excavation, whereby a ~ 200 m long channel is cut through the southern end of Kaitorete spit (near Taumutu). A number of factors affect the success of manual opening events, including lake level, climatic conditions (wind), tidal cycles, wave action (Taylor 1996). The channel remains open until gravel is replaced by tidal cycles and/or southerly storm waves. If the lake closes over before lake levels have been sufficiently lowered, re-opening events continue the risk of flooding is reduced (Kirk & Lauder 2002). The Selwyn District and the Christchurch City Councils manages a further network of drains and lakeside recreation reserves and are responsible for the protection of natural resources in their districts.

1.1.3 Lake management

The lake is subject to a Joint Management Plan between the Department of Conservation and Te Rūnanga o Ngai Tahu (Te Rūnanga o Ngai Tahu 2005). This is a statutory plan which aims for integrated management of the natural and historic resources in the plan area, concomitantly aware of both Mahinga Kai and conservation purposes. There are a number of conflicting issues which complicate management of the lake. Among these are; poor biological health of the lake, the requirements for protection of extant biodiversity, significant cultural values and entitlements to Ngāi Tahu, increased public interest in the lakes ecology, the increased agricultural intensification of the catchment and the effects of continued lake openings. Furthermore, reductions in groundwater levels and tributary inflows will be major concerns for lake managers in the future, as extensive reductions in lake level could have detrimental impacts on all aspects of lake ecology and associated values. There is need for improved management of the lake, because of the wide range of cultural, economic, hydrological and ecological values mentioned above. Recently, a vision for the lake has been proposed, including three scenarios that consider a range of lake values and conflicting issues (Hughey *et al*., 2009). These include; An improved status quo incorporating ongoing (but recent) management initiatives and their maintenance; A realistic and resilient environmentally enhanced future, which is built around a set of achievable, short, medium and long term goals and is based on a compromise between the enhancement of 'natural values' and considerations of technical and economic feasibility; An idealised future based on strict conservation management principles. It will be difficult to establish a management framework that will deliver optimum outcomes for all desired values. Whatever the outcome, tradeoffs are inevitable.

1.1.4 Brackish waters – influence of saline concentration

Most brackish lakes experience regular and predictable fluctuations in salt concentrations due to the mixing of freshwater and saline water. Salinity is an important factor influencing the diversity and structure of invertebrate communities as many species are unable to cope with the associated osmotic stress (James *et al.,* 2003; Kefford *et al.,* 2003; Jeppesen *et al.,* 2007; Waterkeyn *et al.,* 2008; Ellis & Macisaac 2009). Consequently, many studies have found a decrease in invertebrate taxonomic richness as salinity concentrations increase in estuarine environments (Williams *et al.,* 1990; Williams & Williams 1998; Greenwood & Wood 2003; Piscart *et al.,* 2006).

Plants and animals have evolved and adapted to a wide range of aquatic environments and have developed a range of physiological mechanisms and adaption's to maintain the necessary balance of water and dissolved ions in cells and tissues (osmoregualtion). Salinity primarily affects the occurrence of species through its link with osmoregulatory physiology (Hart *et al.,* 1991; Withers 1992). The ability of organisms to maintain optimal internal osmotic concentration against external gradients determines the salinity tolerance of that species. Organisms typically found in saline environments are hypo-osmotic regulators; they are able to maintain lower concentration of solutes than their surroundings through active osmosis. Levels of tolerance to saline concentrations can change throughout the different stages of an organisms life cycle (Hart *et al.,* 1991). Thus, some species are more vulnerable to salinity fluctuations at certain times of the year and this is important for lake managers to consider. For example, Lake Ellesmere/Te Waihora provides important habitat for many avian communities (O'Donnell 1989; Taylor 1996; Hughey & O'Donnell 2009). However, very limited research has been done on the basal food resource (macro-invertebrates) that supports these large bird populations (Taylor 1996; Hughey & O'Donnell 2009). Invertebrates are essential to all life stages of birds, providing protein which is necessary for growth and reproduction (Swanson & Meyer 1977). If at certain life stages invertebrates are more susceptible to salinity, as they are to the effects of drought (Bataille & Baldassarre 1993), then it is possible that opening Lake Ellesmere/Te Waihora to the sea at the wrong time may have major cascade effects through the food chain.

The brackish nature of Lake Ellesmere/Te Waihora is typical of many coastal lakes and results from the mixing of freshwater from a number of rivers (e.g. Selwyn River), marine water influx during lake opening and saline intrusion under and over Kaitorete Spit (Taylor 1996). The frequency and duration of lake openings and relative volumes of fresh and seawater thus has a large influence on salinity concentrations. Climatic variables such as temperature, can also affect salinity concentrations, particularly in summer when higher temperatures increases the rate of evapo-transpiration and salt concentration in shallow regions of the lake. For example, during the drought of 1998-1999, the lake reached its highest annual average salinity concentrations on record (14 ppt), due to reduced freshwater inflows from tributaries and high evaporation rates from the lake (Hayward & Ward 2009). The opening is located at the southern end of the lake and salinity concentrations show marked spatial as well as temporally patterns (Spigel 2009). This contributes to a diverse array of habitats for flora, ranging from freshwater wetland to salt marsh vegetation (Hughey & O'Donnell 2009; Grove & Pompei 2009). Thereby, spatial and temporal variation in lake salinity has the potential to strongly influence the distribution, composition and abundance of fauna within the lake.

1.1.5 Water level fluctuation - influence on lake ecosystems

Altered water-levels and increased water level-fluctuation are among the major anthropogenic disturbances in the littoral zone of lake ecosystems (Richter *et al.,* 1997; Coops *et al.,* 2003). Hydro-power production, the construction of dams, water abstraction for irrigation and artificial manipulation to reduce flooding, have changed the natural hydrological regimes of lakes and river systems worldwide (Dynesius & Nilsson 1994). The temporal patterns (frequency and magnitude) of water level fluctuations can range from seconds to days, and have the potential to drive benthic invertebrate abundance and composition in the littoral zone of lakes (Hofmann *et al*., 2008). Short-term water level fluctuations (minutes - hours), driven by wind or boat wakes, would likely impose relatively minor physical stress on organisms living in the littoral zone. In contrast, long-term water level fluctuations (days – years) driven by lake level management, may place considerable stress on benthic invertebrates by altering habitat availability and exposing communities to extreme environmental conditions (i.e. desiccation). This may result in alterations of the natural hydrologic cycles causing water level fluctuations that surpass the physiological or behavioural adaptability of many organisms (Coops *et al*., 2003; Cott *et al*., 2008). Lake Ellesmere/Te Waihora is influenced by both short and long-term water level fluctuations. Short term changes frequently occur due to strong winds creating waves and generally result in water level shifts of less than 0.5 m (Taylor 1996). This leaves some parts of the littoral zone completely dewatered, while other areas become deeper albeit for a short period of time

(Figure 1.2). Long term changes (days – years) occur through artificial lake openings, resulting in extended areas of the littoral zone experiencing desiccation for longer periods of time. Additionally, extreme climatic events (high temperatures and evapo-transpiration) and the catchments hydrological regime (frequency of floods/drought) can cause dramatic changes in water level. Typically a strong south-westerly wind can cause lake water mass to shift north, significantly reducing water levels at the southern end of the lake (Figure 1.2), and the opposite pattern occurs during a strong north-westerly wind. Manual openings of Lake Ellesmere/Te Waihora reduces water level around the whole lake, and has potentially very different consequences for benthic invertebrates due to the long term shift in water level.

A number of studies have found a variable response of lake biota to the frequency, duration and extent of water levels change (James *et al*., 1998; Baumgärtner *et al.,* 2008; Brauns *et al*., 2008). More extreme fluctuations (change in water level and duration) tend to have the most detrimental effects on biota (Pinay *et al*., 1990; Richardson *et al*., 2002). For example, extensive dewatering of the littoral zone as observed in reservoirs, negatively affects benthic invertebrate abundance by decreasing the available habitat. The shifting wetted area may cause mortality amongst those organisms that cannot migrate or withstand periods of desiccation (Trotzky & Gregory 1974; McAfee 1980; Blinn *et al*., 1995; Prus *et al*., 1999; Richardson *et al*., 2002). Furthermore, exposure to the atmosphere due to fluctuating water levels can stress littoral invertebrates through desiccating or freezing of littoral sediments and vegetation (Coops *et al*., 2003; Leira & Cantonati 2008). Thus water level fluctuations can have varying impacts in littoral zones depending on the frequency, extent and duration and are more deleterious to benthic communities at low lake levels. Therefore, perhaps a minum lake level needs to be set over summer months in Lake Ellesmere/Te Waihora in order to protect benthic invertebrate communities.

Figure 1.2 Lake Ellesmere/Te Waihora A) Normal water level at Taumutu (1130 hrs 24th June 2008). B) Extremely strong SE wind (1300 hrs 24th June 2008). C) Greenpark Sands high water level (May 2009). D) Greenpark sands, after lake opening event (August 2009).

1.1.6 Contextual summary and thesis outline

Coastal lake ecosystems are under increasing pressure from anthropogenic activities. A thorough understanding of the ecology of littoral benthic invertebrate communities and their response to environmental factors is important for lake managers to assess the multiplicative effects of human activities. Benthic invertebrates constitute a significant biomass and are recognised as playing an important role in overall production of lake ecosystems. Lake Ellesmere/Te Waihora is highly nutrient enriched, largely modified by water level manipulation and undergoes frequent saline intrusions. The lake has been artificially opened and water levels manipulated for at least 60 years. To date there are no records of the basic response of lake biota to these lake opening disturbances. Lake Ellesmere/Te Waihora is an important resource for a wide range of users, and the degraded nature of the lake has caused concern. Current research focuses on trying to understand factors driving lake degradation and possible restoration measures. Such studies include the potential to re-establish macrophyte beds (Jellyman *et al.,* 2009), factors affecting water clarity (Gerbeaux & Ward 1991), food wed links (Wood *et al*., 2008; Kelly & Jellyman 2007) and phytoplankton biomass (Larned & Schallenberg 2006). To my knowledge there have been no studies on how the basal food resource, benthic invertebrate fauna respond to fluctuating water levels and salinity concentrations. These are the two key issues upon which my thesis is focused; how do lake level fluctuations and salinity concentrations influence invertebrate community structure and diversity in the littoral zone of Lake Ellesmere/Te Waihora?

Specifically my objectives were to investigate the following questions:

- How do fluctuating water levels relate to water chemistry?

- How do fluctuating water levels relate to benthic invertebrate community structure in the littoral zone? Is there a difference in community structure from the shore out into the lake?

- Is salinity a factor restricting the presence of some species within the invertebrate community (e.g. invertebrate predators)?

Chapter 2

Human impacts on water quality and hydrology of Lake Ellesmere/Te Waihora

2.1 Abstract

Lake Ellesmere/Te Waihora is a nationally important coastal, brackish lake in New Zealand. However, impacts from climatic and anthropogenic pressures have led to a degradation of water quality. I investigated water quality patterns spatially and temporally around the lake using a combination of field and laboratory assessments. Results suggest water quality in Lake Ellesmere/Te Waihora is in a hypertrophic state, due to high nutrient (nitrogen and phosphorus) concentrations resulting in high chlorophyll *a* levels. Water chemistry conditions varied spatially, with the eastern most end having generally the best water quality and lowest salinity. Mean concentrations of total nitrogen ranged from 1.63 to 2.4 mg/L, chlorophyll *a* from 50 to 148 *u*g/L, total suspended solids from 151 – 248 mg/L and mean salinity from 4.9 – 6.9 ppt. Seasonally, highest nutrient concentrations (mean, TN = 2.625 mg/L, DRP = 0.059 mg/L and TP = 0.365 mg/L) occurred in late summer months (February – March), slightly decreasing but remaining high throughout winter. The lack of significant relationships between water quality variables and water level, and the positive relationship between chlorophyll a and salinity, suggests lake opening events are not effective at improving water quality or reducing phytoplankton biomass. A higher water level, together with reduced nutrient loading, would benefit water quality health in the long-term in Lake Ellesmere/Te Waihora.

2.2 Introduction

In New Zealand many ecological studies and monitoring have largely focused on deep lakes (Hamill 2006). However, there appears to be increasing interest in shallow coastal lakes, due to their decreasing water quality state, changes in hydrology, and location in regards to anthropogenic pressures (Drake *et al.,* 2009: Schallenberg *et al*., 2010). This chapter describes the current state of water quality in Lake Ellesmere/Te Waihora, and considers the impact of lake hydrology on the salinity regime.

2.2.1 Pressures on lake ecosystems

Anthropogenic activities such as agriculture intensification and urbanisation have been identified as the main contaminant contributors to lake systems. These activities combined with water level manipulation can greatly accelerate degradation of water quality, habitat quality and ecosystem functioning (Table 2.1). Eutrophication through an increase in nutrient load, is the dominant stressor in most lakes globally, though in some areas such as the North American Great Lakes, acidification has been the key detrimental factor (Parsons *et al.,* 2010). Furthermore, invasive pests (plants and animals) can place considerable pressure on lake ecosystems by displacing native species and altering biological communities. Invasive vascular macrophytes are widely distributed in New Zealand lakes and frequently exclude lower growing native plants (Vant 1987). Trout have displaced and reduced the abundances of many native animal species (Fish 1966; McDowall 1968) and bottom feeding activities of fish such as European Koi Carp (*Cyprinus carpio*) can degrade water quality by increasing turbidity (Hanchet 1990). In Lake Ellesmere/Te Waihora the spread of gray and crack willow has reduced extent of native freshwater wetland vegetation around the lake shore over the last 25 years (Pompei & Grove 2009). Lakes in highly populated or intensively cultivated areas have experienced dramatic increases in nutrient loading and sedimentation, resulting in turbid water and losses of biodiversity (Wetzel 2001). Several studies have shown that increased nutrient levels markedly influence the structure of littoral invertebrate communities (Tolonen *et al.,* 2001) and suggest a large flow-on effect of eutrophication. Thus, in many countries, reducing external nutrient loading has become the main target for lake managers (Søndergaard *et al.,* 2007). Lowland lakes are particularly susceptible to degradation, owing to their location in the lower portions of their catchments, where they act as a receptacle for accumulated contaminants from upstream. Furthermore, shallow lakes are more at risk from eutrophication as there is a larger interface between the photic zone and the lake bed. Therefore, substances and processes in sediments can influence the water column to a much greater extent (Schallenberg 2004; Qin *et al.,* 2007).

Table 2.1 Common anthropogenic activities and their most important ecological effects on lake ecosystems

Anthropogenic activity	**Type of impact**	Ecological effects	**References**
Agricultural development and activity	Eutrophication Nutrient loading Bacteria Inputs Agrichemicals Sediment	Increased nutrients stimulate phytoplankton production, resulting in algal blooms that reduce water clarity and light availability for submerged macrophytes and periphyton: causes reallocation of primary production from the benthic to pelagic zone: causes hypolimnetic dissolved oxygen depletion due to organic matter decomposition: can result in fish deaths and unpleasant odours. Growth of aquatic plants can become extensive when nutrient concentrations increase and create serious nuisance for lake users, interfering with swimming, boating and other recreational activities.	Carpenter *et al.,* 1998; Scheffer 2001; Vadeboncoeur *et al.,* 2003; Garn *et al*; Egertson *et al*., 2004 Chandra *et al*., 2005: Scheffer & van Nes 2007; Søndergaard & Jeppesen 2007
Water level regulation - Irrigation - Flood protection - Power generation	Alteration of hydrological regime	Affects habitat quality by erosion, causes habitat loss through desiccation in the eulittoral zone and habitat gain in high water levels. Alters seasonal hydrological regime.	Fernández-Aláez *et al*., 1999; Hofmann *et al*., 2008; Keto *et al.,* 2008; Wantzen *et al.,* 2008;
Urbanisation - Shoreline development	Structural development	Reduces habitat heterogeneity through habitat loss or removal; disrupts natural connectivity between littoral and riparian area. Contaminant inputs via urban storm-water systems	Traut & Hostetler 2003; Francis & Schindler 2006
Riparian clear-cutting	Structural degradation	Reduces amount of allochthonous organic matter supplied by riparian vegetation, increases siltation of habitats. Increases in accumulation and/or re-suspension of sediments can be detriment to water quality and habitat for many aquatic species. Reducing wind shelter and shading, thus increasing wind disturbance and temperatures.	Christensen *et al*., 1996; Francis & Schindler 2006

2.2.2 Hydrology

Water quality of lake systems and their hydrology are important aspects driving lake ecosystem functioning. Lake Ellesmere/Te Waihora is the largest shallow-coastal lake in New Zealand, with an average depth of 2 metres. However, the size of the lake has drastically reduced from 30 000 hectares to approximately 20 250 hectares due to agricultural development and efforts to reduce flooding of the surrounding catchment over the last 60 years (Taylor 1996; Hemmingsen 1997; Kirk & Lauder 2000). Over 40 streams and rivers feed into the lake, including six main tributaries; the Selwyn River (Waikirikiri), Irwell River

(Waiwhio), LII River, Halswell (Huritini), Harts Creek (Waitatari) and Kaituna River. The lake is also fed from groundwater recharged from two main sources: rainfall events on the plains, and subterranean seepage from the Rakaia and Waimakariri rivers (Williams 2009). Lake Ellesmere/Te Waihora's major tributary, the Selwyn River drains 276, 000 hectares of land, which has undergone substantial land use change, from an extensive wetland to intensive farmland since 1850. Increased demand for irrigation and climatic conditions, such as reduced rainfall, have resulted in lower ground water levels and lower flows in tributaries, including the Selwyn River, in the past 10 years (Hayward 2007; Hayward & Ward 2009; Williams 2009). Lower inflows to the lake could severely affect invertebrate fauna in the littoral zone, with potentially large flow on consequences to the fisheries of the lake. Variability in rainfall and increased use of groundwater and surface water for irrigation, could restrict freshwater inputs into the lake, and when coupled with increased evaporation, further reduced lake levels could have long lasting dentrimental effects on overall lake health.

2.2.3 Nutrients

The general state of lake water quality and the degree of nutrient enrichment is primarily described by mean annual trophic state. Total nitrogen (TN) and total phosphorus (TP) concentrations are commonly used as indicators of lake trophic status because they include dissolved and readily available nutrients, plus nutrients attached to particles and those contained within phytoplankton cells (Burns *et al.,* 2000). The trophic level index (TLI) developed for lakes in New Zealand, is based on four key water quality determinants (total nitrogen, total phosphorus, chlorophyll a and secchi depth) and has a trophic scale increasing from ultra-microtrophic to hypertrophic as nutrients, algae biomass increase and water clarity declines (Burns *et al.,* 2000). Increasingly, lowland lakes in New Zealand are becoming more nutrient-enriched (Drake *et al.,* 2009). Lake Ellesmere/Te Waihora has high concentrations of nutrients (nitrogen and phosphorus), and poor water clarity (Hayward & Ward 2009). The lake has been classed as hypertrophic for the entirety of the 17 years that water quality data have been available. However, unlike other enriched lakes, Lake Ellesmere/Te Waihora does not display many of the associated characteristics typical of eutrophic lakes (Table 2.1). For example, the lake does not regularity undergo severe oxygen depletion and associated fish deaths, nor does it produce persistent toxic algal blooms, unlike neighbouring Lake Forsyth/Te Roto O Wairewa, which is also classified as hypertrophic (Hayward & Ward

2009). However, in March 2009 the lake experienced a toxic blue-green cyanobacterial bloom of *Aphanocapsa* and *Nodularia* species and in summer 2010, high bio-volume counts of cyanobacteria *Merismopedia* species were recorded although not at toxic levels (ECan, unpublished data). Despite poor water quality, Lake Ellesmere/Te Waihora remains a highly productive lake, and although there have been declines in fish biomass, it still supports substantial fish biomass and maintains a large bird population (Kelly & Jellyman 2007; Hughey & O'Donnell 2009). There is much interest and debate among local community, fishery, wildlife, recreation and Tāngata Whenua groups about how to best to protect the lake from further water quality degradation (Hughey & Taylor 2009).

2.2.4 Salinity

Lake Ellesmere/Te Waihora has undergone major changes since its formation 3000 years ago. The lake was initially a major discharge point for the Waimakariri River, and subsequently has switched back and forth between being a tidal estuary and a freshwater lake, to its current state; an intermittently open and closed brackish lake (Kirk 1994; Hemmingsen 1997). Historically, the lake was fresher and opened naturally once water levels were high enough to naturally breach the Kaitorete gravel barrier (~ 4 m; Taylor 1996). Maori were also known to have opened the lake using horse-drawn scoops whenever water levels threatened to flood shoreline settlements (Taylor 1996). Since 1982, lake opening events have been controlled manually (opening currently occurs when water levels reach a depth of 1.05 m in summer and 1.13 m in winter at Taumutu recorder) and the pattern and duration of openings have been greatly altered from the natural state. These changes have resulted in a more brackish environment and a lower average lake level (~ 1 m; Kirk & Lauder 2000). The brackish nature of the lake is typical of many coastal lakes and results from natural mixing of freshwaters from a number of river inflows (e.g. Selwyn River) and marine water inflows during lake opening and saline intrusion through Kaitorete Spit. The frequency and duration of lake openings and the relative volumes of freshwater and seawater have a large influence on salinity concentrations. Climatic variables such as temperature, can also affect salinity concentration, particularly in summer when higher temperature increases the rate of evapo-transpiration and resulting salt concentration in shallow regions of the lake. For example, during the drought of 1998-1999, the lake reached its highest annual average salinity concentrations on record, due to reduced freshwater inflows from tributaries and high evaporation rates from the lake (Hayward & Ward 2009). As the lake opening is at the southern end, salinity concentrations show marked spatial and temporal patterns (Spigel 2009). These contribute to diverse habitats for flora and fauna, including many wetland bird species, and vegetation ranging from freshwater wetland to salt marsh (Hughey & O'Donnell 2009; Grove & Pompei 2009). Spatial and temporal variation in lake salinity influences the distribution, composition and abundance of flora and fauna within the lake.

2.2.5 Management

Lake Ellesmere/Te Waihora is subject to a Joint Management Plan between the Department of Conservation and Te Rūnanaga o Ngai Tahu. This is a statutory plan, which aims for integrated management of the natural and historic resources in the plan area, for Mahinga Kai and conservation purposes. Environment Canterbury is responsible for water-quality monitoring in the lake and tributaries, pest management, and maintaining a system of tributary drains in the Halswell Drainage District.

In order to determine if environmental conditions influence benthic invertebrate community patterns in Lake Ellesmere/Te Waihora, I investigated spatial and temporal water quality conditions around the lake. Specifically I addressed the following questions:

1. Are there spatial differences in water quality around the lake? How does Lake Ellesmere/Te Waihra's water quality compare to other coastal lakes?
2. Are there seasonal differences in nutrients concentrations?
3. How does lake level change (specifically lake opening events) relate to water quality?
4. Does saline intrusion have any effect on water quality parameters?

2.3 Methods

2.3.1 Water quality sampling

Monthly water quality samples have been taken from four sites in the western area of the lake since 1993 as part of Environment Canterbury's long term monitoring programme (Figure 2.1; Table 2.2). In addition, I established, two more sampling sites (at Kaituna Lagoon and Greenpark Sands) on the eastern side, in order to gain a better understanding of spatial differences around the lake (Figure 2.1; Table 2.2). The four long-term monitoring sites were sampled by boat, by Environment Canterbury's water quality field staff. On the same day, the two additional sites were sampled from the lake shore.

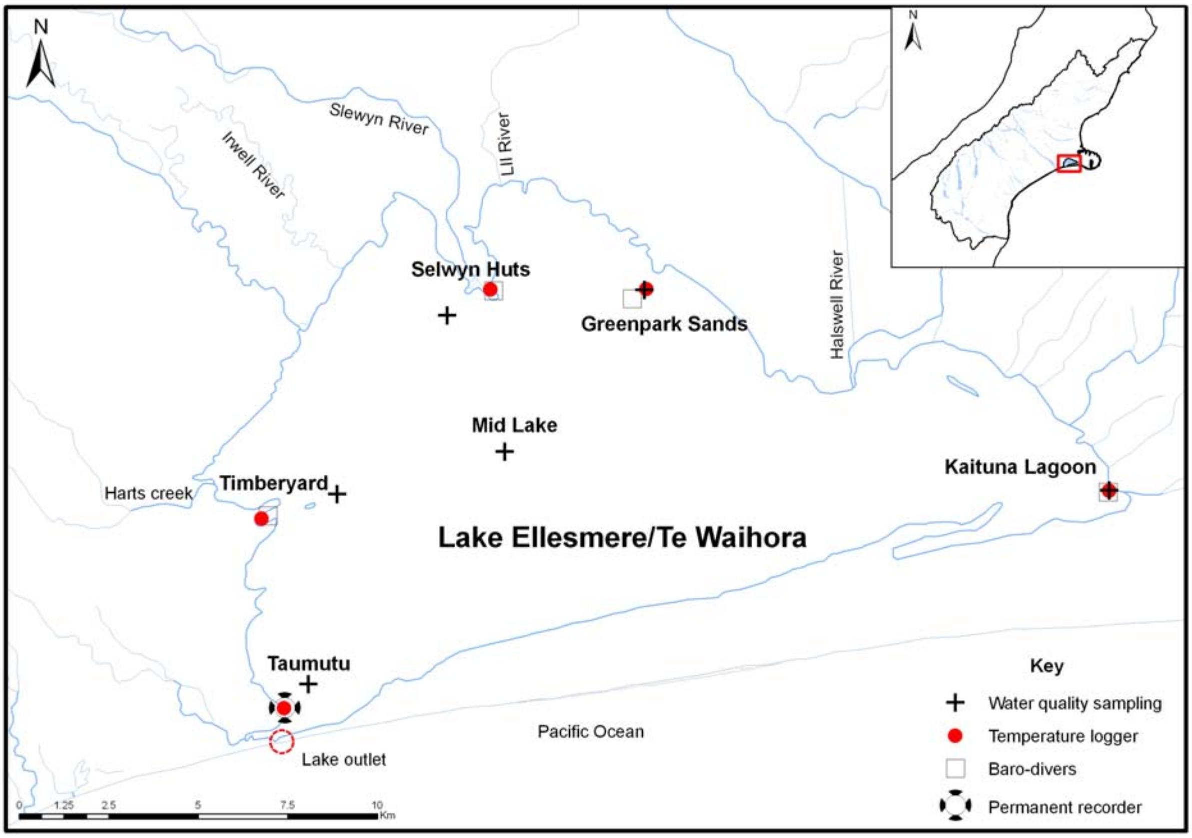


Figure 2.1 Location of water quality sampling sites, water level recorders and temperature loggers on Lake Ellesmere/Te Waihora.

Water quality samples were collected from the lake edge with an extended grabber pole (~2 m long). Containers were placed just below the surface (~30 cm) until full, immediately capped, chilled and returned to the Environment Canterbury Water Quality Laboratory (Christchurch, IANZ accredited) for analysis. Samples were analysed for nitrogen and phosphorus in their particulate/organic and dissolved forms and also total suspended solids (Table 2.2). Phytoplankton biomass was assessed by estimating chlorophyll a using the flurometric method (APHA 10200). Additionally, field observations were made of wind direction and strength, rainfall, water clarity (measured using a secchi disc) and number of birds within a ~100 m radius. Spot data were collected for dissolved oxygen concentration and saturation, temperature and salinity using Pro DOPTO (Model 3100) and YSI (Model 30) meters. The dissolved oxygen meter (Pro DOPTO Model 3100) automatically adjusted measurements for respective dissolved oxygen concentration, dissolved oxygen saturation and temperature once a salinity value was entered.

Monthly water quality data were collected from January to December 2009 at Selwyn Huts, Timberyard, Mid Lake and Taumutu, from February to December 2009 at Kaituna Lagoon, and from February to October at Greenpark Sands. Where appropriate, water quality determinants from the six sites were averaged to provide an overall indication of Lake Ellesmere/Te Waihora water quality. Monthly water quality data collected by Environment Canterbury from January to December 2009 from three coastal lakes (Forsyth/Wairewa, Coopers Lagoon/Muriwai and Wainono Lagoon) were also analysed for comparison with Lake Ellesmere/Te Waihora.

Table 2.2 Water quality monitoring locations and water quality determinants monitored monthly around Lake Ellesmere/Te Waihora (WQ = water quality).

Lake Ellesmere/Te Waihora	Location	Parameter	Monitoring
Selwyn Hutt's	Off Selwyn River mouth	WQ	Monthly 1993
Timberyard	South of Timberyard point	WQ	Monthly 1993
Mid Lake	Mid Lake	WQ, salinity logger	Monthly 1993; Jan 2009
Taumutu	Taumutu near recorder	WQ; salinity logger	Monthly 1993; Jan 2009
Kaituna Lagoon	Off SH75	WQ	Monthly February 2009
Greenpark Sands	End of Jarvis Road	WQ	Monthly February 2009

Parameter	Abbreviation	Detection Limit	Unit
Water temperature	TEMP	±1 %	°C
Secchi depth	Secchi		m
Suspended solids	SS	0.1	mg/L
Ammonia-nitrogen	NH3N	0.005	mg/L
Nitrate+nitrite nitrogen	NNN	0.005	mg/L
Total nitrogen	TN	0.08	mg/L
Dissolved reactive phosphorus	DRP	0.001	mg/L
Total phosphorus	TP	0.008	mg/L
Chlorophyll *a*	Chl *a*	0.1	*u* g/L
Salinity	Salinity	± 1 %	ppt

2.3.2 Salinity and temperature loggers

Environment Canterbury have had two salinity loggers installed at Mid Lake and Taumutu since 2007 (Figure 2.1; Table 2.2). Environment Canterbury staff maintained the sites and downloaded data at the same time they collected monthly water quality samples. During 2009 the data-loggers recorded salinity at 15 minute intervals.

In order to combine and utilise water quality data collected by Environment Canterbury, I established three of my five transects in relation to their sampling locations (Selwyn Huts, Timberyard and Taumutu; Figure 2.1). Two more sampling locations were established in order to obtain spatial representation around the lake (Kaituna Lagoon and Greenpark Sands; Figure 2.1). At each of the five sampling locations (Kaituna Lagoon, Greenpark Sands, Selwyn Huts, Timberyard and Taumutu), a transect perpendicular to the lake edge was established (Figure 2.2). This transect consisted of a gradient of three sites from the eulittoral lake shore out into the lower littoral zone based on water depth and substrate (Figure 2.2). The lower littoral zone was located at a depth which was expected to remain under water for most of the year. At each site in the littoral zone, a water level gauge was secured to a steel warratah and temperature loggers were attached 10 cm above the substrate. The length of the transect varied with location and lake bed angle, but ranged from 40 m at Taumutu to 1.2 km at Greenpark Sands. Temperature loggers (HOBO Pendant temp UA-001-08) were placed at the littoral zone sites around the lake to provide an indication of the frequency of wetting and drying, and diurnal temperature fluctuations. Loggers recorded temperature at 30 minute intervals from January to March 2009. The detection range of temperature loggers in water was from 0°C to 50°C with an accuracy of ± 0.47°C at 25°C. Due to extreme climatic conditions, loss of loggers and difficulty collecting at high water level, use of loggers was not continued after their collection in March 2009. Instead, semi-permanent barometric divers were installed in the lower littoral zone to record water level change (refer Chapter 3).

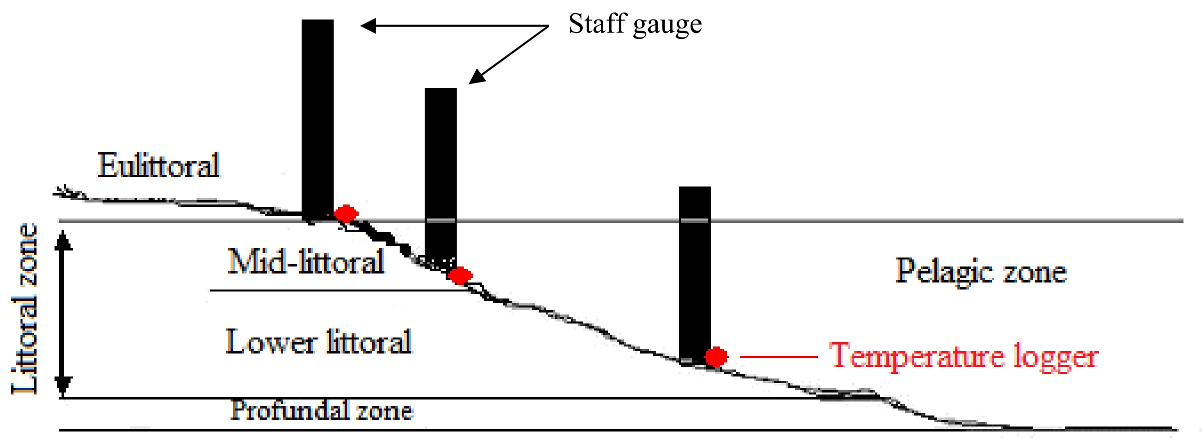


Figure 2.2 Three sampling locations along a transect from the lake shore out into the lake.

2.3.3 Data Analysis

Where water chemistry concentrations were below or above the laboratory detection limits, results were reported as ‘less than’ (i.e. < 0.08) or ‘greater than’ (i.e. > 2400). The ‘less than’ results were converted to a value equal to half the detection limit (i.e. < 0.08 = 0.04) and the ‘greater than’ results were given a value equal to the upper detection limit (i.e. > 2400 = 2400; Scarsbrook & McBride 2007). Water quality data are presented in box and whisker plots, which portray the mean value as a line, mean ± SE as outer edges of a box, and minimum and maximum as the outer ends of the whiskers, produced in Statistica (V7). These distributions illustrate significant differences between representative data sets within the lake and can be related to water quality guidelines to identify potential issues of concern. One-way analysis of variance (ANOVA), with Tukey's multiple comparison test, were used to test for differences between sites, and linear regressions were used to examine relationships between water quality variables and water level in Prism (V6). Values were considered significant when $p < 0.05$. Before analysis, water quality data were checked for normality and log transformed (x+1) to stabilise the variance when necessary (Quinn & Keough 2002). For analysis of seasonal effects, months were grouped as follow; summer (December – March), autumn (April-May), winter (June-August), spring (September-November).

2.4 Results

2.4.1 Temperature and dissolved oxygen

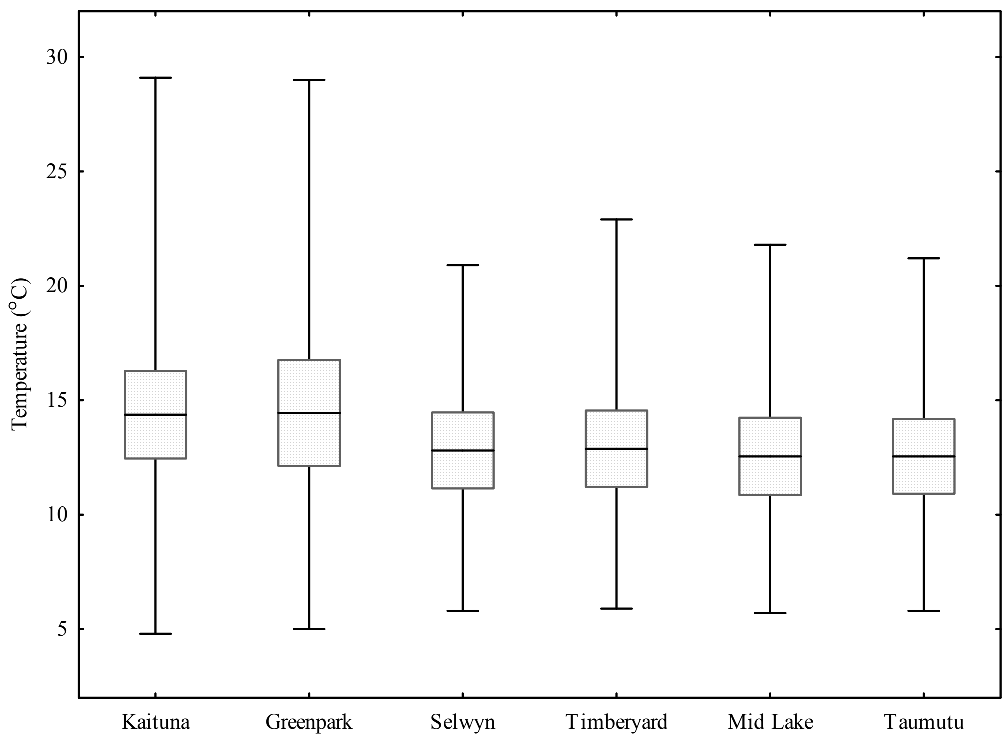
Spot monthly water temperature measurements were similar at all sites around the lake on any one day, and did not significantly differ between sites (One-way ANOVA, $F_{5, 64} = 0.22$, $P = 0.952$; Figure 2.3A). Temperature showed a predictable seasonal pattern being warmest in summer (max = 29 ºC) and coolest in winter (min = 5 ºC).

Dissolved oxygen saturation values were generally above the guideline value for protection of aquatic ecosystems of 80% saturation (ANZECC 2000; Appendix 1). The exception to this was at Kaituna Lagoon, where dissolved oxygen saturation frequently fell below 80%. Dissolved oxygen concentrations did not differ significantly between sites around the lake (One-way ANOVA $F_{5, 64} = 1.59$, $P = 0.176$).

2.4.2 Suspended solids and clarity

Total suspended solids concentration ranged from 27 to 620 mg/L (Figure 2.3B). Kaituna Lagoon had the lowest mean suspended solids (225 mg/L) and Greenpark Sands the greatest range in concentrations (84 – 620 mg/L), including some very high readings on occasions (Figure 2.3B). The south-western sites, Mid Lake and Taumutu, generally had the highest suspended solid concentrations. One-way ANOVA showed no significant difference in suspended solids spatially or seasonally in the lake ($F_{5,68} = 1.74$, $P = 0.139$; $F_{11,57} = 1.59$, $P = 0.127$). Despite the lack of statistical significance, some seasonal patterns could be seen in the data. Total suspended solids concentrations were generally higher in late summer (towards the end of March) and lowest over winter (May through August); concentrations were particularly low in winter at Greenpark Sands and Kaituna Lagoon.

Measurements of secchi depth were similar across the lake with mean values of ~0.1 m. Not surprisingly, water clarity was similar, both spatially and seasonally, to suspended solids, with Greenpark Sands showing the greatest variation in water clarity, and improved clarity in winter.



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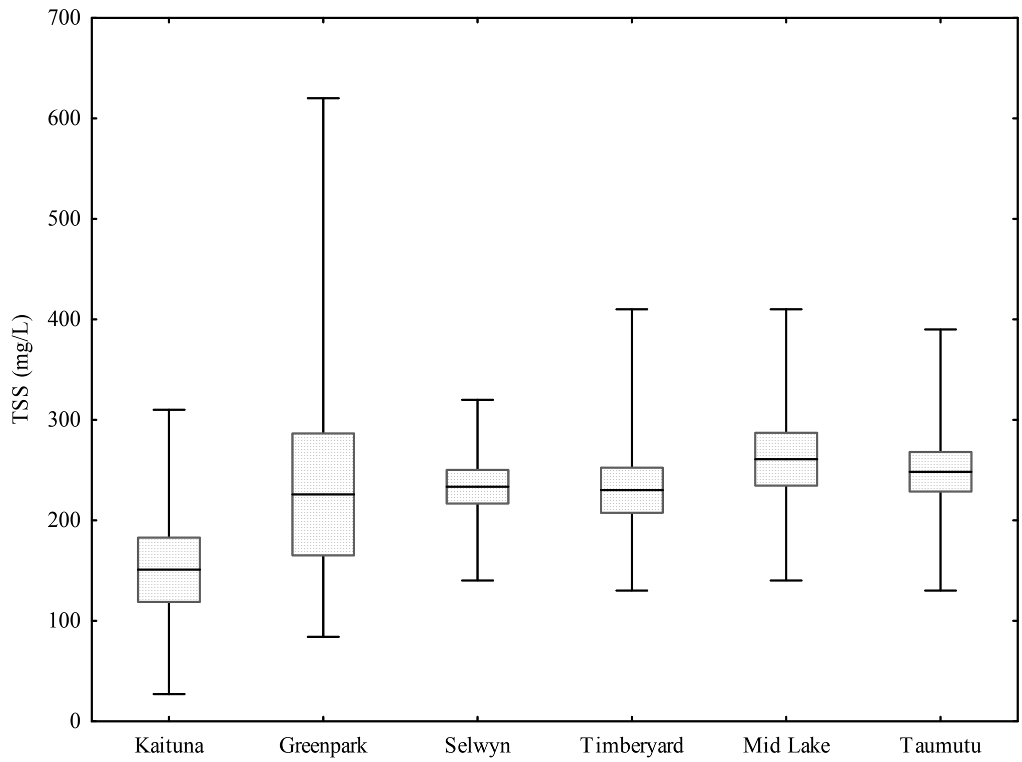


B

Figure 2.3 A) Spot measurements of water temperature collected around Lake Ellesmere/Te Waihora over 2009 B) Monthly suspended solids concentration at six sites in Lake Ellesmere/Te Waihora over 2009.

2.4.3 Nutrient concentrations

Greenpark Sands had the highest mean ammonia nitrogen concentration (NH_3-N = 0.053 mg/L) and greatest range in concentrations (Figure 2.4A). In contrast, Taumutu had the lowest mean ammonia nitrogen concentration (NH_3-N = 0.009 mg/L) (Figure 2.4A). Ammonia nitrogen concentrations varied significantly around the lake (One-way ANOVA, $F_{5,63} = 3.26$, $P = 0.011$; Figure 2.4A; Table 2.3A). Concentrations of NH_3-N were significantly higher at Greenpark Sands than Kaituna, Timberyard, Mid Lake and Taumutu (Table 2.3A). Seasonally, NH_3-N concentrations varied on a month by month basis (One-way ANOVA, $F_{11,56} = 5.47$, $P < 0.0001$), being highest in summer (February) and winter (August) months. When grouped into seasons no significant difference was observed ($F_{3,64} = 0.211$, $P = 0.888$).

Mean nitrite and nitrate nitrogen (NNN) concentrations were similar across all sites, except for Mid Lake (Figure 2.4B). Timberyard had the highest mean concentration (NNN = 0.053 mg/L) and greatest range in concentrations (0.0025 – 0.28 mg/L; Figure 2.4B). NNN concentrations did not vary significantly between sites (One-way ANOVA, $F_{5, 63} = 0.741$, $P = 0.545$), but significant seasonal patterns were observed (One-way ANOVA, $F_{3,64} = 5.029$, $P = 0.003$; Table 2.3B). NNN concentrations were significantly higher in autumn and winter than summer (Table 2.3B).

Total nitrogen (TN) concentrations ranged from 0.86 – 3 mg/L, with mean values falling above or close to the hypertrophic boundary threshold value of 1.56 mg/L (Burns *et al.,* 2000) or very close to it at all sites (Figure 2.4C). There was significant variation in TN around the lake ($F_{5,62} = 4.081$, $P = 0.003$; Table 2.3A). Kaituna lagoon had significantly lower TN concentrations than Greenpark Sands, Selwyn Huts, Timberyard, Mid Lake and Taumutu (Table 2.3A). TN concentration also varied seasonally ($F_{3,64} = 6.201$, $P = 0.0009$; Table 3B) with significantly highest concentrations over summer and autumn than spring months (Figure 2.5A; Table 2.3B).

TN concentrations were similar to Lake Ellesmere/Te Waihora, in three other coastal lakes in south Canterbury; Lake Forsyth/Wairewa, Coopers Lagoon/Muriwai and Wainono Lagoon. Total nitrogen concentrations were above the hypertrophic boundary threshold value in Coopers Lagoon/Muriwai and Wainono Lagoon (Figure 2.4C). However, although Lake Forsyth/Wairewa had a low median TN value (mean = 1.55 mg/L), it had the greatest range in values. Lake Ellesmere/Te Waihora, Coopers Lagoon/Muriwai and Wainono Lagoon followed a similar seasonal pattern, with fairly consistent TN concentrations that were slightly higher in winter. Although, Lake Forsyth had highest TN concentrations in January through March, TN concentrations decreased during the remainder of the year (Figure 2.5B). Mean TN concentration differed significantly between the four lakes (One-way ANOVA $F_{3,44} = 3.578$, $P = 0.021$; Table 2.3C), but no effect of season was detected ($F_{11,36} = 0.658$, $P = 0.767$). Lake Forsyth/Wairewa had significantly lower TN concentrations than Coopers Lagoon/Muriwai (Table 2.3C).

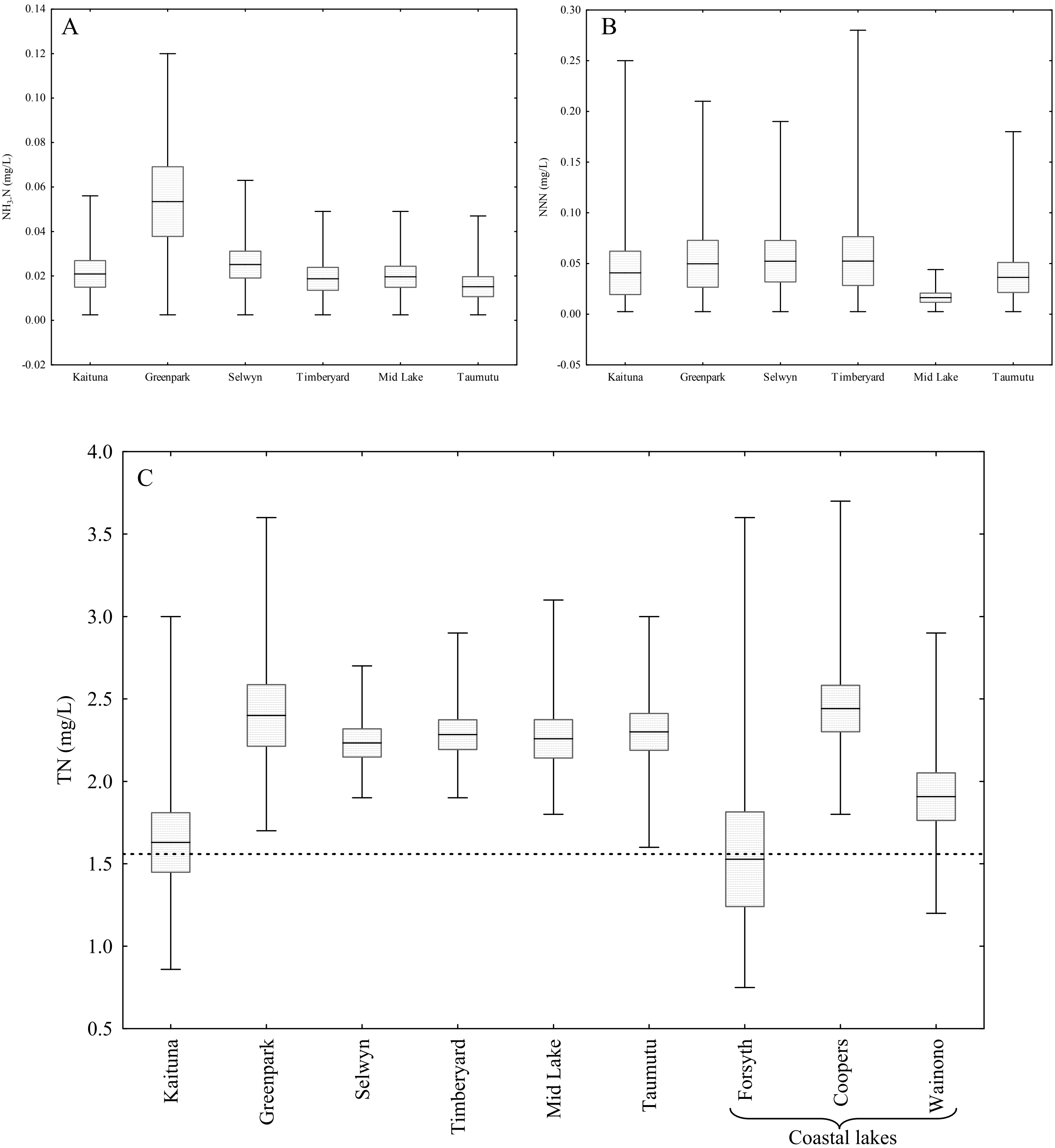
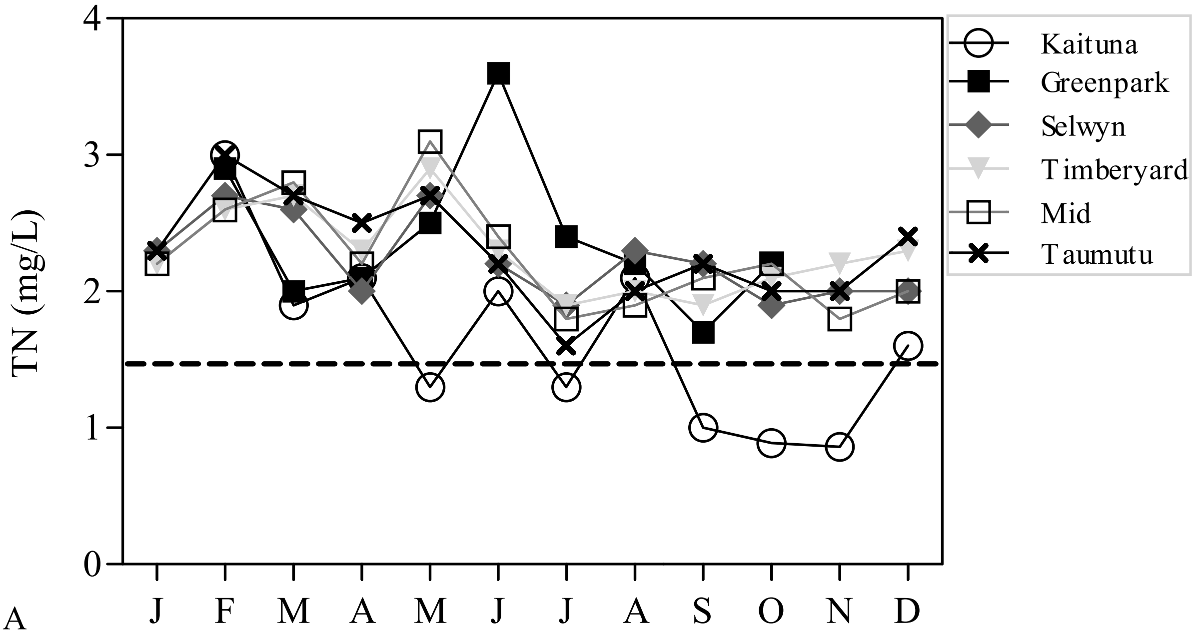


Figure 2.4 Nitrogen concentrations collected monthly in 2009 at six sites in Lake Ellesmere/Te Waihora: A) Ammonia nitrogen (NH_3-N) B) Nitrate nitrite nitrogen (NNN) C) Total nitrogen (TN). Data for three coastal lakes in South Canterbury are also shown in C in which the dashed line indicates the hypertrophic guideline value of 1.56 mg/L (Burns *et al.,* 2000).



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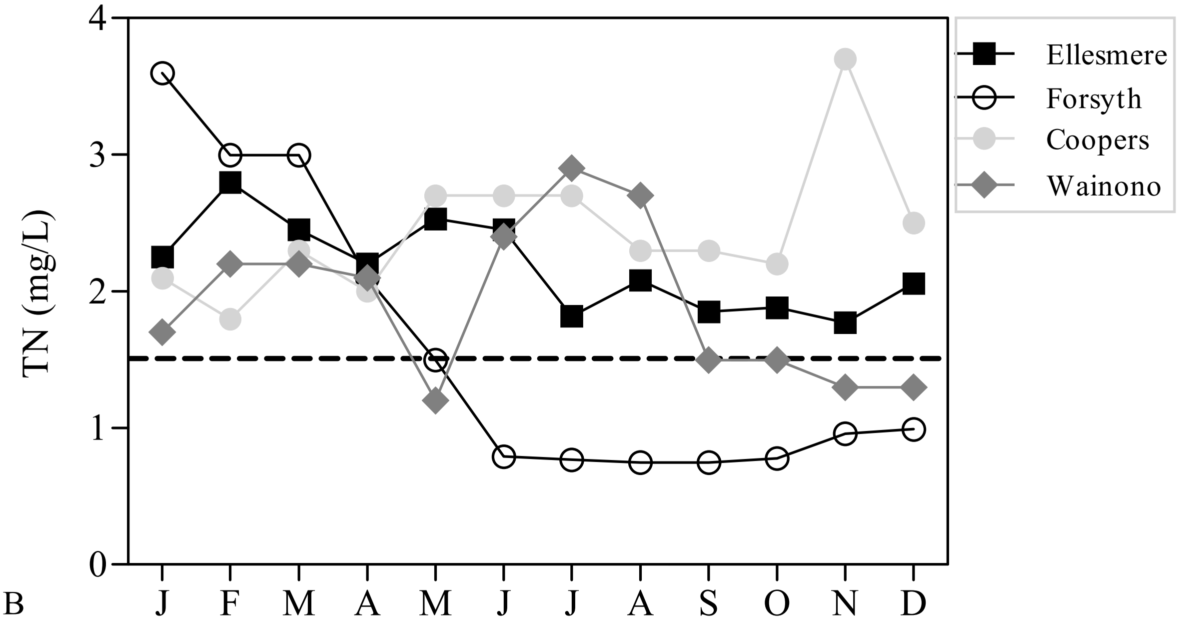

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Figure 2.5 Mean monthly concentrations of total nitrogen in 2009: A) For six sites in Lake Ellesmere/Te Waihora, B) Mean TN concentrations for Lake Ellesmere/Te Waihora, and the three coastal lakes in South Canterbury. The dashed line indicates the hypertrophic boundary value of 1.56 mg/L as in Figure 2.4.

Table 2.3A Results of one-way ANOVAs testing differences in 3 water quality parameters among sites in Lake Ellesmere/Te Waihora, January – December 2009.

Spatial Difference	**NH_3-N**		**TN**		**Chl. a**	
One-way ANOVA	$F_{5,63} = 3.26$	$P =$ **0.011**	$F_{5,62} = 4.081$	$P =$ **0.003**	$F_{5,62} = 4.081$	$P =$ **0.0005**
Turkey's Test	q-value	*P*- value	q-value	*P*- value	q-value	*P*- value
Kaituna vs Greenpark	4.213	**< 0.05**	5.368	**< 0.01**	2.308	> 0.05
Kaituna vs Selwyn	0.577	> 0.05	4.511	**< 0.05**	4.229	**< 0.05**
Kaituna vs Timberyard	0.320	> 0.05	4.891	**< 0.05**	4.945	**< 0.05**
Kaituna vs Taumutu	0.816	> 0.05	5.018	**< 0.01**	4.218	**< 0.05**
Kaituna vs Mid	0.192	> 0.05	4.701	**< 0.05**	6.773	**< 0.001**
Greenpark vs Timberyard	4.597	**< 0.05**	0.841	> 0.05	2.329	> 0.05
Greenpark vs Taumutu	5.066	**< 0.01**	0.721	> 0.05	1.641	> 0.05
Greenpark vs Mid	4.476	**< 0.05**	1.021	> 0.05	4.060	> 0.05

Table 2.3B Results of one-way ANOVAs testing differences in nutrient concentrations among seasons in Lake Ellesmere/Te Waihora, 2009.

Seasonal Difference	**NNN**		**TN**		**DRP**		**TP**	
One-way ANOVA	$F_{3,64} = 5.029$	$P =$ **0.003**	$F_{3,64} = 6.201$	$P =$ **0.0009**	$F_{3,64} = 6.039$	$P =$ **0.001**	$F_{3,64} = 9.645$	$P =$ **0.0001**
Tukey's Test	q-value	*P*- value	q-value	*P*- value	q-value	*P*- value	q-value	*P*- value
Summer vs Autumn	4.469	**< 0.05**	0.461	> 0.05	0.724	> 0.05	1.969	> 0.05
Summer vs Winter	4.704	**< 0.01**	2.996	> 0.05	3.899	**< 0.05**	3.899	**< 0.05**
Summer vs Spring	2.342	> 0.05	5.665	**< 0.05**	5.394	< 0.01	7.64	**< 0.001**
Autumn vs Winter	0.2848	> 0.05	2.135	> 0.05	2.657	**> 0.05**	1.449	> 0.05
Autumn vs Spring	2.262	> 0.05	4.46	**< 0.001**	3.972	< 0.05	4.722	**< 0.01**
Winter vs Spring	2.208	> 0.05	2.62	> 0.05	1.5	**> 0.05**	3.668	> 0.05

Table 2.3C Results of one-way ANOVAs testing differences in TN, TP and chlorophyll *a* concentrations between Lake Ellesmere/Te Waihora and 3 coastal lakes in South Canterbury, January – December 2009.

Spatial - Coastal Lakes	**TN**		**TP**		**Chl. a**	
One-way ANOVA	$F_{3,44} = 3.578$	$P =$ **0.021**	$F_{3,44} = 10.71$	$P <$ **0.0001**	$F_{3,44} = 25.83$	$P <$ **0.0001**
Turkey's Test	q-value	*P*- value	q-value	*P*- value	q-value	*P*- value
Ellesmere vs Forsyth	3.072	> 0.05	2.289	> 0.05	5.392	**< 0.01**
Ellesmere vs Coopers	1.353	> 0.05	7.356	**< 0.001**	11.360	**< 0.001**
Ellesmere vs Wainono	1.351	> 0.05	0.969	> 0.05	9.732	**< 0.001**
Forsyth vs Coopers	4.425	**< 0.05**	5.067	**< 0.01**	5.968	**< 0.001**
Forsyth vs Wainono	1.721	> 0.05	1.320	> 0.05	4.340	**< 0.05**
Coopers vs Wainono	2.704	> 0.05	6.387	**< 0.001**	1.627	> 0.05

Dissolved reactive phosphorus (DRP) concentrations were similar across all sites, with concentrations ranging from 0.005 – 0.11 mg/L (Figure 2.6A). Mean total phosphorus (TP) concentrations at all sites exceeded the hypertrophic boundary threshold value of 0.096 mg/L (Burns *et al.,* 2000; Figure 2.6B). No significant difference of either DRP or TP concentrations between sites in the lake were found ($F_{5,63} = 0.165$, $P = 0.975$; $F_{5,63} = 0.79$, $P = 0.56$, respectively). Seasonally, the highest concentrations of both DRP and TP were observed in summer, decreasing through the remainder of the year (Figure 2.7A). DRP and TP concentrations were significantly higher in summer than winter and spring, and in autumn compared to spring (Table 2.3B).

Lake Ellesmere/Te Waihora had similar TP concentrations to Forsyth/Wairewa and Wainono Lagoon. All three lakes showed elevated mean TP concentrations above the hypertrophic boundary threshold value of 0.096 mg/L (Burns *et al.,* 2000; Figure 2.6B). In contrast, Coopers Lagoon/Muriwai had low TP concentrations, well below the eutrophic boundary threshold value of 0.02 mg/L (Figure 2.6B). TN significantly differed between the four lakes ($F_{3,44} = 10.71$, $P = 0.0001$; Table 2.3C), but no seasonal effect ($F_{11,36} = 1.084$, $P = 0.4$; Figure 2.7B). Coopers Lagoon had significantly lower TP concentrations than the other three lakes (Table 2.3C).

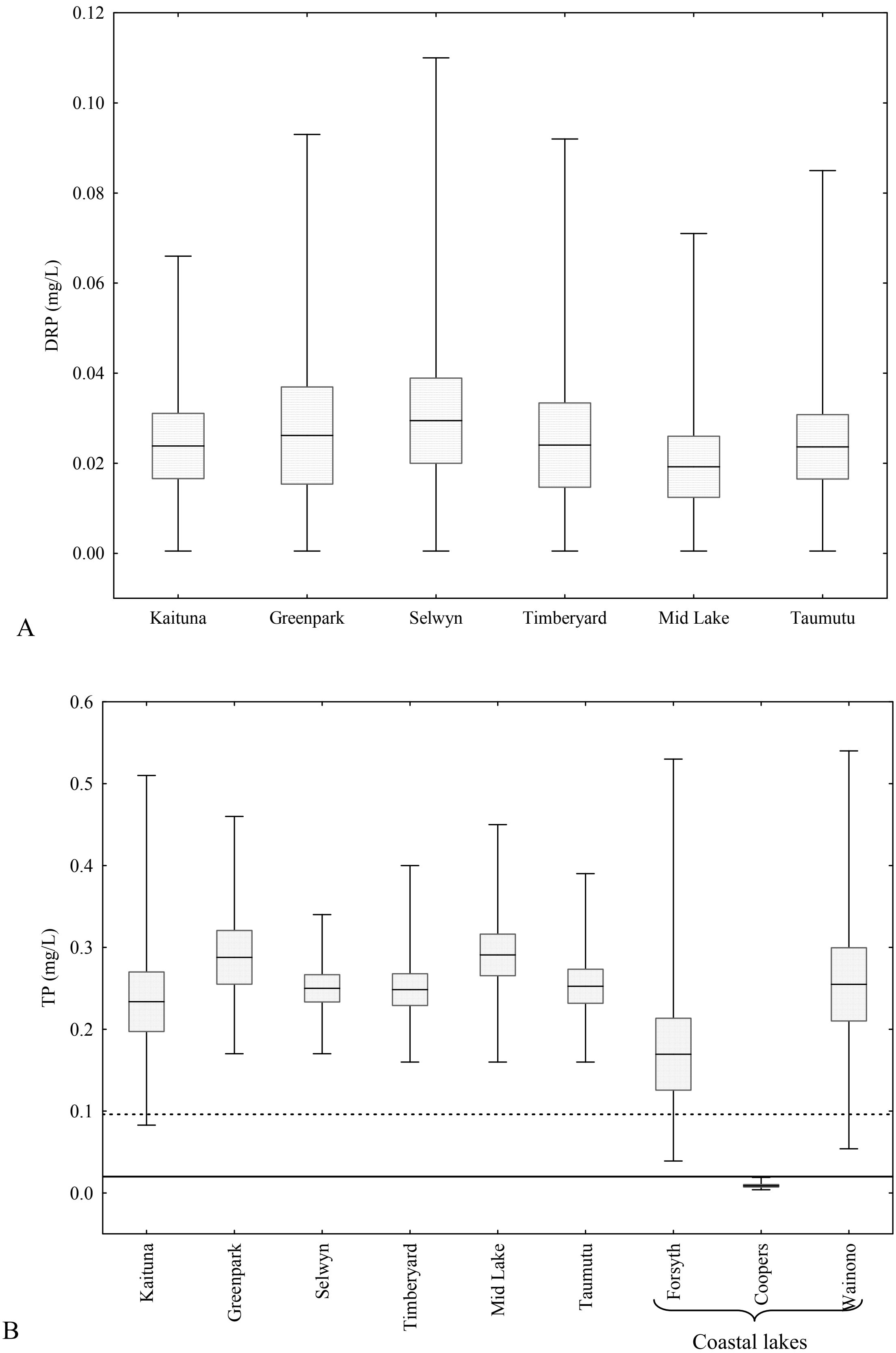


Figure 2.6 Phosphorus concentrations collected monthly in Lake Ellesmere/Te Waihora in 2009. A) DRP, B) TP. values for three coastal lakes in south Canterbury are also shown in B. Dashed line = 0.096 mg/L hypertrophic boundary, solid line = 0.02 mg/L eutrophic boundary (Burns *et al.,* 2000).

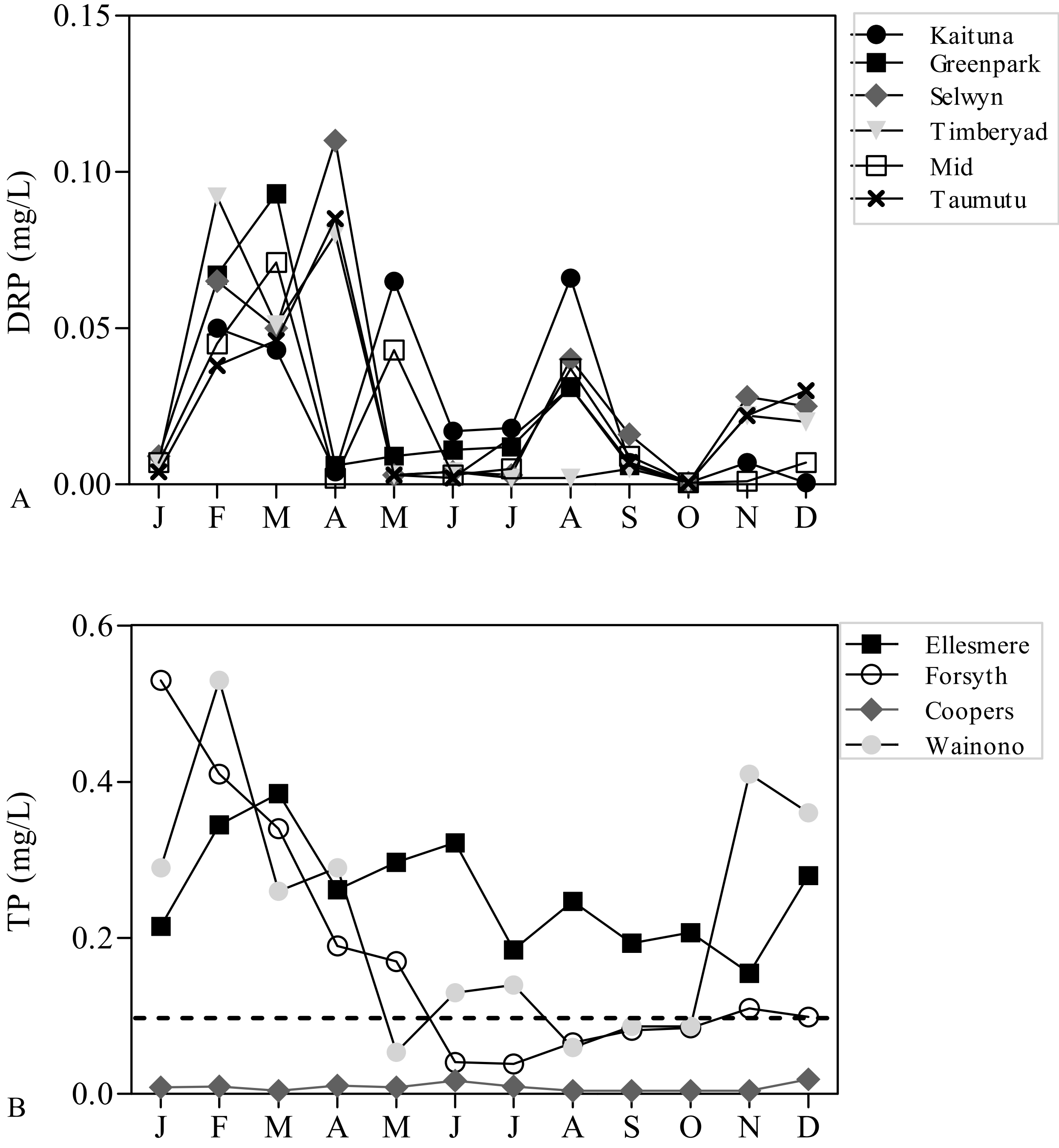
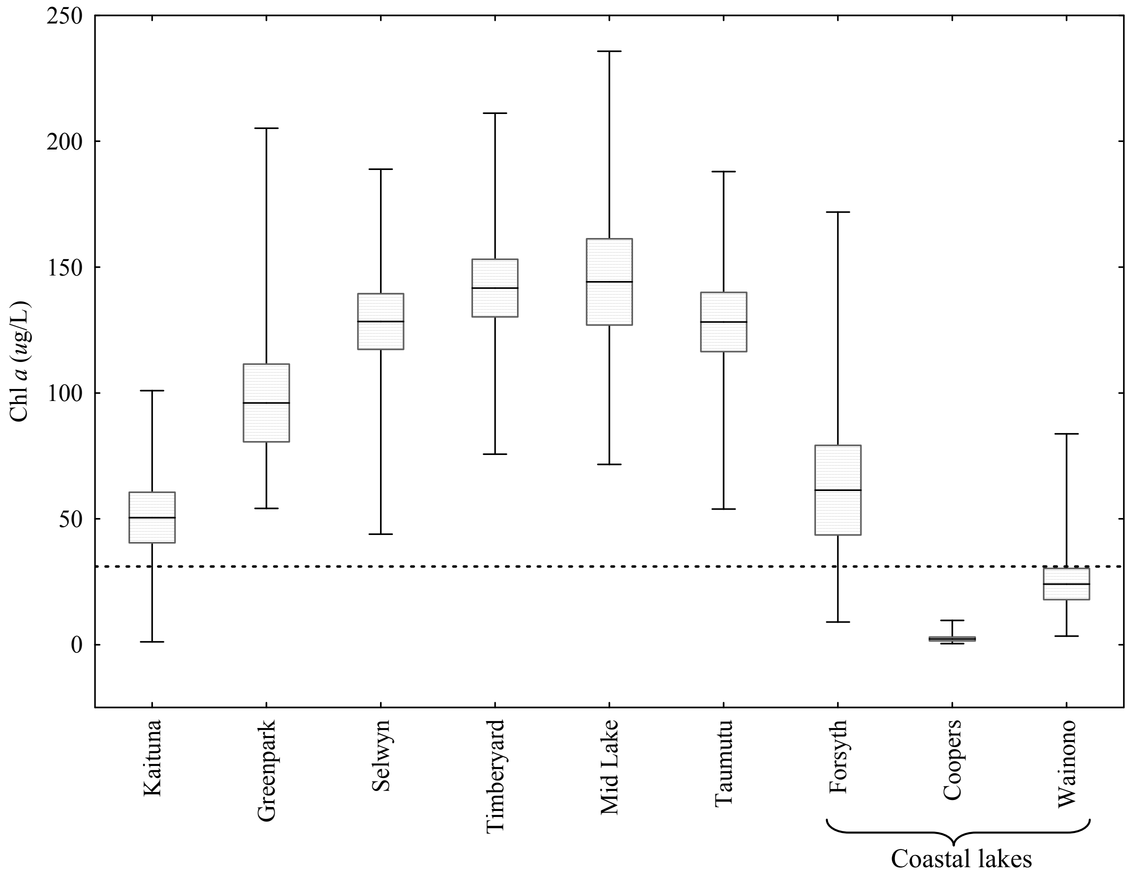


Figure 2.7 Monthly phosphorus concentrations. A) DRP concentrations at six sites in Lake Ellesmere/Te Waihora: B) TP concentrations at four coastal lakes in south Canterbury. The dashed line indicates the hypertrophic boundary threshold of 0.096 mg/L (Burns *et al.,* 2000).

2.4.4 Chlorophyll a

Chlorophyll *a* concentrations were high at all lake sites (Figure 8). Mean concentrations greatly exceeded the hypertrophic boundary threshold concentration of 31 *u*g/L (Burns *et al.,* 2000; Figure 2.8A). Highest mean concentrations were found at the Mid-Lake site (mean = 144 *u*g/L), and the lowest were in Kaituna Lagoon (mean = 50 *u*g/L; Figure 2.8A). Chlorophyll *a* concentrations significantly varied around the lake (One-way ANOVA ,$F_{5,62} = 5.228$, $P = 0.0005$; Table 2.3A), but no seasonal effect was found ($F_{11,56} = 0.791$, $P = 0.648$; Figure 2.8B). Kaituna Lagoon had significantly lower chlorophyll *a* concentrations than all other sites except Greenpark Sands (Table 2.3A).

Lake Ellesmere/Te Waihora had similar chlorophyll *a* concentrations to Lake Forsyth/Wairewa. In contrast, Coopers Lagoon/Muriwai and Wainono Lagoon had low chlorophyll a concentrations (Figure 2.8A). Chlorophyll *a* concentrations significantly differed between the four lakes (One-way ANOVA, $F_{3,44} = 25.83$, $P < 0.001$; Table 2.3C). Tukey's tests showed Lake Ellesmere/Te Waihora had significantly higher concentrations than Lake Forsyth, Coopers Lagoon and Wainono Lagoon (Table 2.3C). Chlorophyll *a* concentrations were significantly higher in Forsyth than Coopers Lagoon and Wainono (Table 2.3C).



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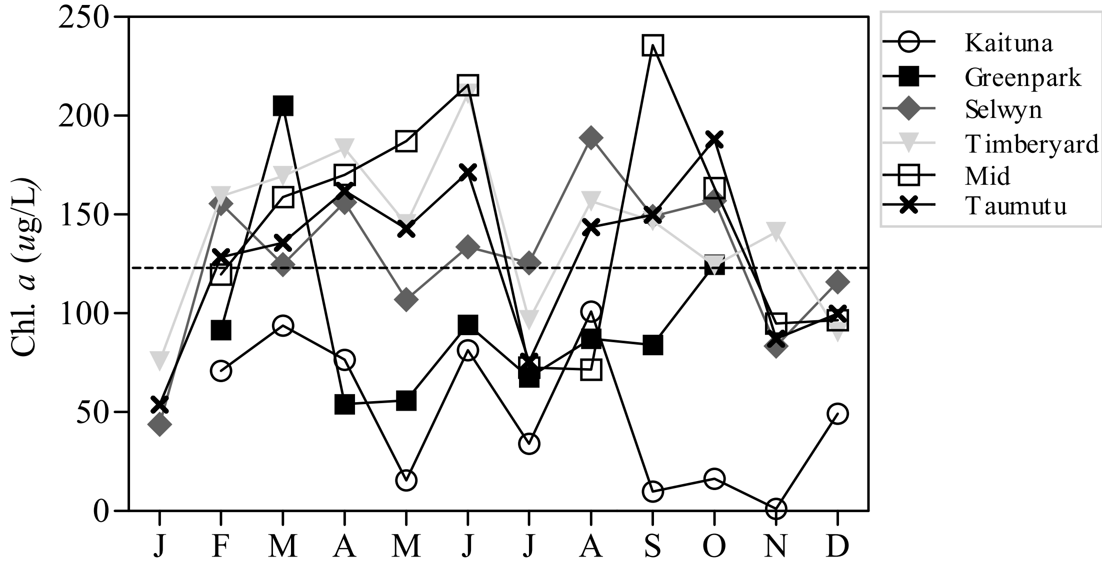

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Figure 2.8 Chlorophyll a concentrations in Lake Ellesmere/Te Waihora based on monthly collections in 2009: A) At 6 sites and in three other coastal lakes, B) Monthly Chl a data for the 6 sites. Dashed line = the hypertrophic boundary threshold of 31 *u*g/L.

2.4.5 Trophic level Index

Lake Ellesmere has high nutrient concentrations, high algal biomass and poor water clarity, which together give it a classification of hypertrophic (Table 2.4). Since 1997, total nitrogen concentrations have shown the greatest mean increase from 2.02 – 2.18 mg/L, along with total phosphorus and chlorophyll *a* (Table 2.4).

Table 2.4 Trophic status of Lake Ellesmere/Te Waihora 2009 (Burns *et al*., 2000).

Hypertrophic	Chl *a* (ug/L) >31	Secchi depth (m) <0.4	TP (mg/L) >0.096	TN (mg/L) >0.1558	Trophic Level >6
Mean 1997	85	0.13	0.197	2.02	7.8
Mean 2009	120	0.1	0.26	2.18	8
Mean 97-09	95	0.13	0.248	2.216	7.9

2.4.6 Controls on phytoplankton growth

Chlorophyll *a* (Chl. *a*) concentration was positively related to total nitrogen concentration ($r^2 = 0.55$, $P < 0.0001$; Figure 2.9A) and total phosphorus ($r^2 = 0.42$, $P < 0.0001$; Figure 2.9B), suggesting that phytoplankton comprised a relatively constant proportion of the TN and TP pools. Chlorophyll *a* concentrations were negatively related to secchi depth ($r^2 = 0.203$, $P = 0.002$; Figure 2.9C), salinity ($r^2 = 0.3$, $P < 0.0001$: Figure 2.9D) and total suspended solids ($r^2 = 0.53$, $P < 0.0001$). Salinity had a positive influence on the Chl. *a*: TN ratio ($r^2 = 0.27$, $P < 0.0001$: Figure 9D) and on the Chl. *a*: TP ratio ($r^2 = 0.3$, $P < 0001$; Figure 2.9E).

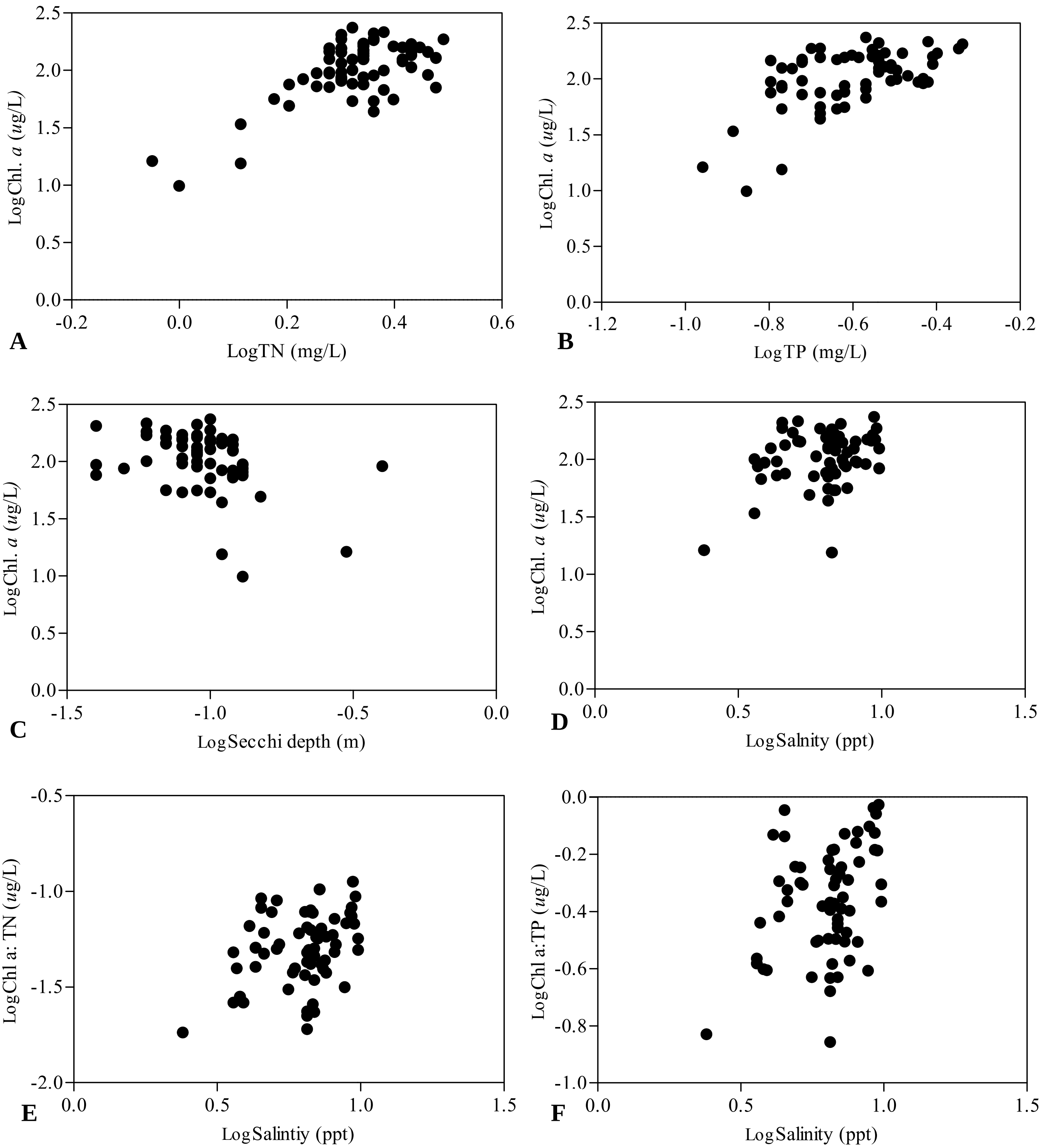
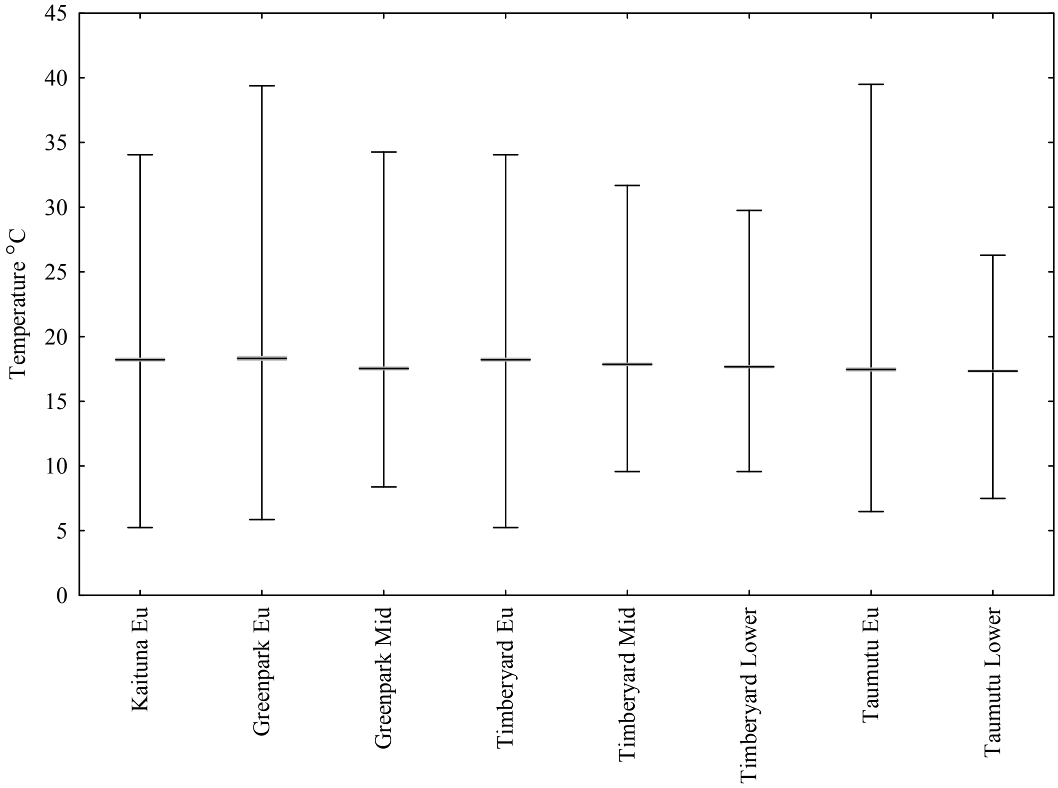


Figure 2.9 Linear regressions of chlorophyll a concentration against A) Total nitrogen. B) Total phosphorus. C) Secchi depth and D) Salintiy. D) Salinity; and the chlorophyll a: TN ratio. F) salinity; and the chlorophyll a: TP ratio.

2.4.7 Temperature

Of the fourteen temperature loggers that were deployed in the lake, eight were collected and six were lost or damaged. Mean temperature records were similar around the lake and showed distinct diel fluctuations (Figure 2.10), with warmest temperatures during the day (1100 – 1700 hrs) and coolest temperatures at night (0100 – 0800 hrs). Coolest temperatures were recorded in the eulittoral zones, (i.e. Kaituna Lagoon, minimum 6°C), where the warmest temperatures were also found (i.e. Greenpark Sands and Timberyard, maxima 39°C, air temperature due to water level drawdown). All eulittoral zone sites showed a greater range in temperatures than mid-littoral and lower sites (Figure 2.10A). The largest difference in temperature along the littoral zone transect was observed over summer.



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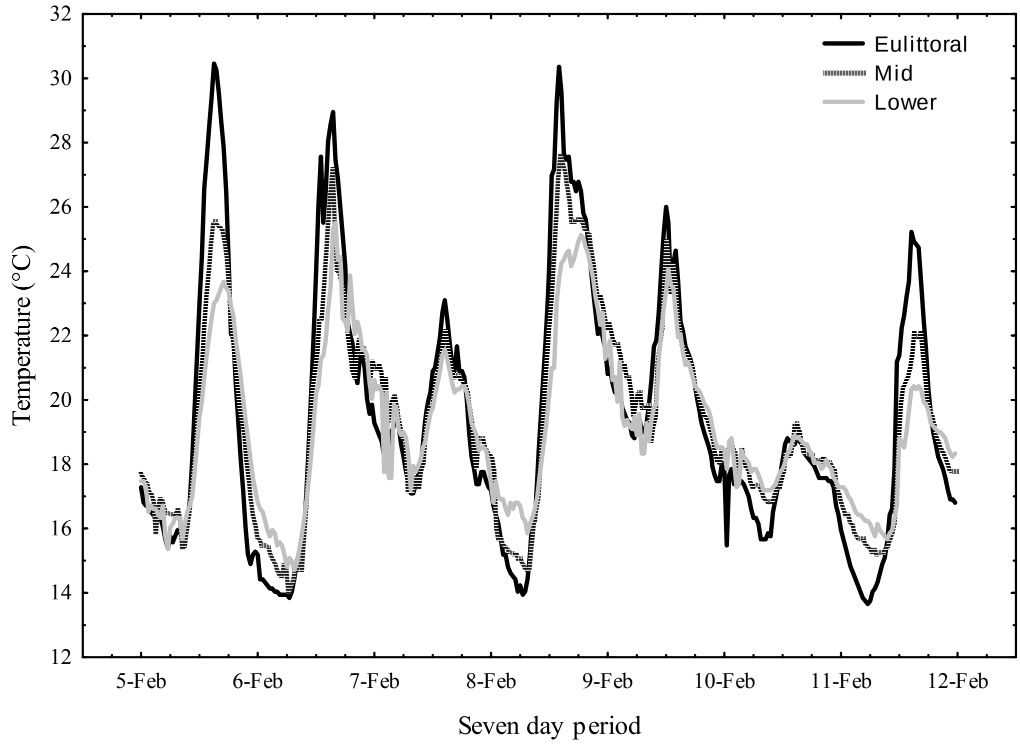

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Figure 2.10 A) Temperature data from January – March 2009 at four littoral zone sites in Lake Ellesmere/Te Waihora (Eu = Eulittoral, Mid = Mid and Lower = Lower littoral zone). B) Temperature data over a 7 day period in the littoral zone at Timberyard in February 2009.

2.4.8 Salinity

Spot salinity concentrations varied spatially and temporally throughout the lake. They ranged from near freshwater at Kaituna Lagoon (0.7 ppt) to high brackish (almost full seawater = 35 ppt) at Taumutu (27 ppt; Figure 2.11). Highest salinities were recorded predominately at Taumutu after the lake had been successfully opened and inundated by seawater (Figure 2.12). One-way ANOVA showed a significant difference between spot salinity concentrations around the lake ($F_{4,98} = 4.214$, $P = 0.0034$). Tukey's test showed Taumutu and Kaituna were most different ($q = 5.674$, $P < 0.01$). Lake Forsyth/Wairewa had a similar salinity regime to Lake Ellesmere/Te Waihora, whereas Coopers Lagoon/Muriwai and Wainono Lagoon were barely brackish (Figure 2.11).

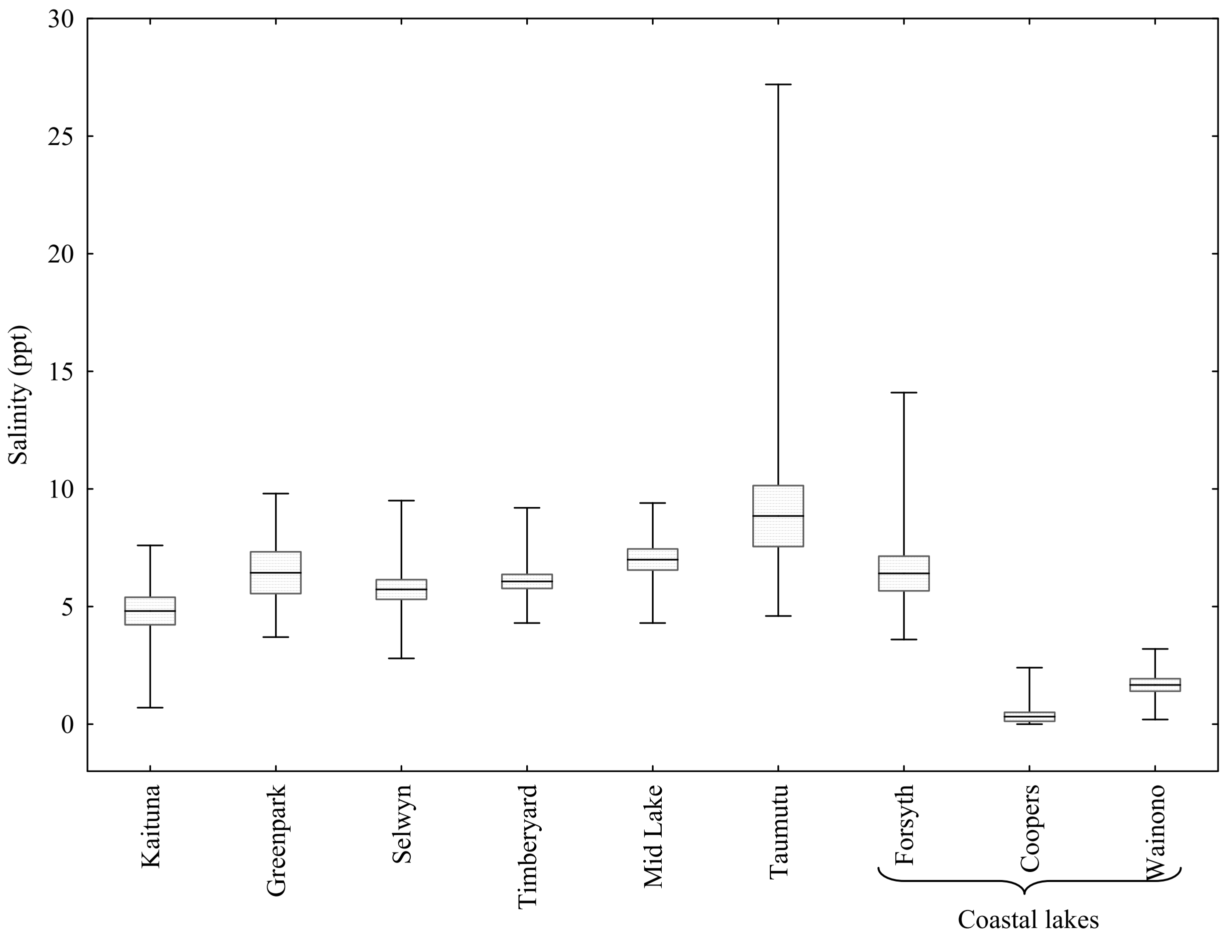
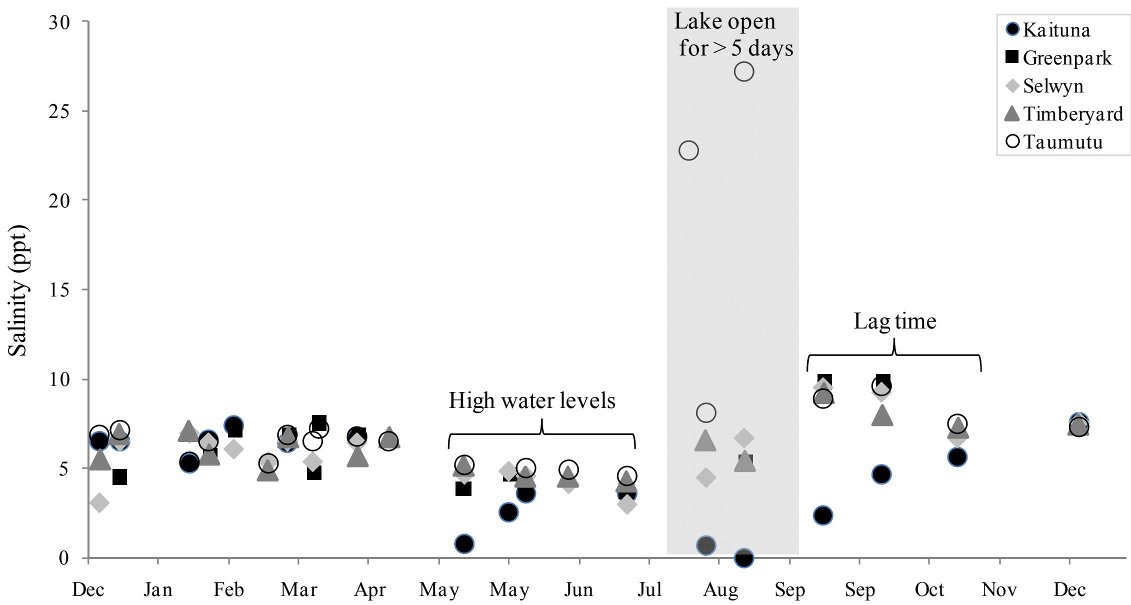


Figure 2.11 Spot salinity data collected at six sites on Lake Ellesmere/Te Waihora in2009 and data for three other coastal lakes in south Canterbury.

Temporal variation in salinity occurred in conjunction with seasonal variations. Lowest salinity concentrations occurred at high lake water levels when the lake was closed and there had been high rainfall (flooding) in the catchment. These effectively diluted salinity concentrations (Figure 2.12). Short-term fluctuations in salinity were observed at the south-west end (Taumutu), as a result of high seas and strong south-easterly winds that caused seawater to overtop the gravel barrier (Figure 2.12B). However, increases in salinity around the rest of the lake were not as marked as those at the south-western end, due to the large volume of lake water buffering infrequent short-term fluctuations (Figure 2.12). Spot salinity measurements showed no significant effect of season ($F_{3,55} = 0.839$, $P = 0.478$). However, as salinity can fluctuate on a daily to weekly basis it is likely monthly salinity measurements did not accurately represent fluctuating salinity concentrations around the lake. This is further shown from the 15 minute interval salinity data (Figure 2.13A).

Salinity data from Mid Lake and Taumutu loggers show that concentrations varied on a short-term (daily) and long-term basis (> 5 days; Figure 2.13A). At Taumutu, short term fluctuations occurred during lake openings (and seawater exchanges) and when the sea overtopped the gravel barrier. For example, over a 48 hour period in February 2009, concentrations at Taumutu ranged from 3.4 to 33 ppt. However, the response was considerably more muted at the Mid Lake site, which was 8.6 km away from the barrier, and only after a prolonged period of opening with significant amount of seawater exchange, did marked salinity changes occur there. There was also a lag in response time, as it takes time for the inflowing seawater to mix throughout the lake (Figure 2.12B & 2.13A). Wind is also likely to drive the rate of saline mixing throughout the lake. A weak but highly significant relationship was shown by linear regression analysis between salinity and water level at Taumutu ($r^2 = 0.14$, $P < 0.0001$; Figure 13B). At lower water levels (when the lake was open) salinity was higher; conversely, at higher water levels salinity concentrations were lower (Figure 2.13B).



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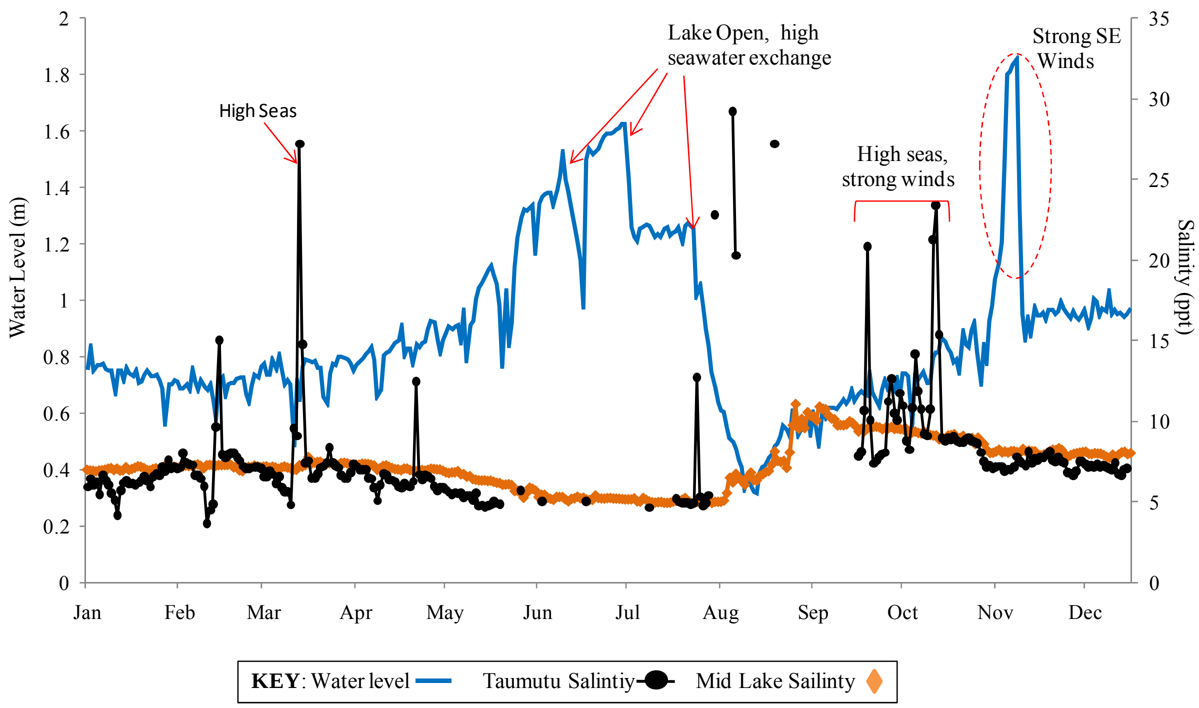

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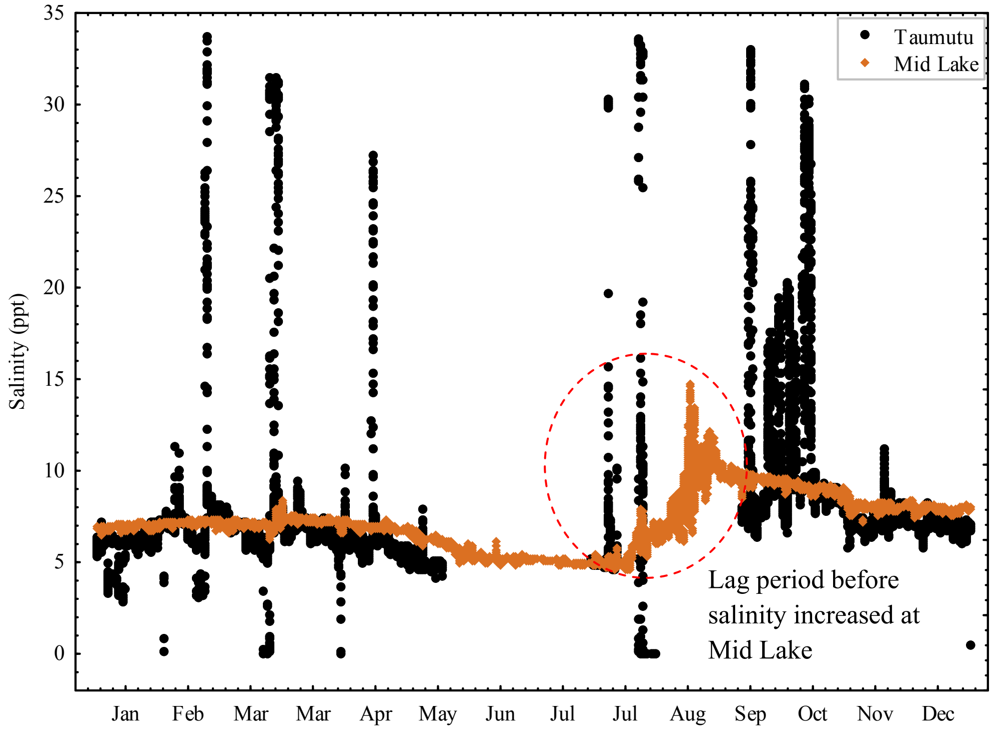
Figure 2.12 A) Spot salinity measurements at five sites around Lake Ellesmere/Te Waihora January – December 2009. B) Daily mean water level and daily mean salinity concentration at Taumutu and Mid Lake, January-December 2009 (Data provided by Environment Canterbury).



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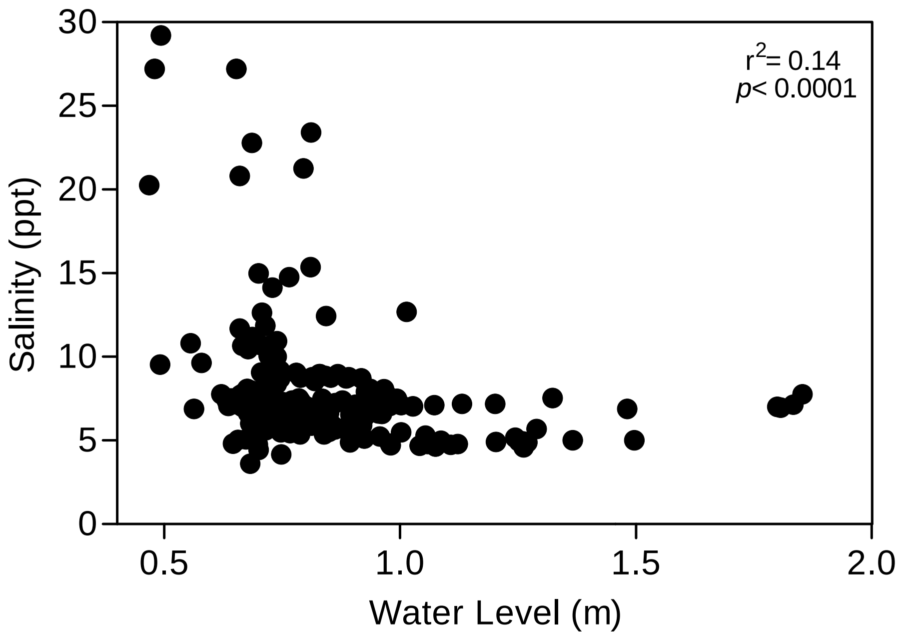

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Figure 2.13 A) Continuous salinity concentrations (15 min interval) at two sites on Lake Ellesmere/Te Waihora January-December 2009. B) Relationship between continuously logged salinity and daily water level at Taumutu January-December 2009.

2.4.9 Relationship between water level and water quality

Of the seven water quality parameters analysed, two were positively related to water level. Log transformed ammonia nitrogen concentration, showed increased concentrations at low and high water levels and lower concentrations at intermediate water levels (r^2 = 0.27, P = 0.004; Figure 2.14A). The r^2 from linear regression, although low, showed suspended solids concentrations were higher at lower water levels (r^2 = 0.11, P = 0.004; Figure 2.14B). Concentration ratios of Chl. *a* and the ratios *Chl*. *a*: TN and Chl. *a*: TP generally remained high irrespective of lake level (Figure 2.14), as were NNN and DRP. Temperature and dissolved oxygen concentrations were significantly negatively related to water level (Temp: r^2 = 0.158, P = 0.0008; DOSAT: r^2 = 0.206, P < 0.0001).

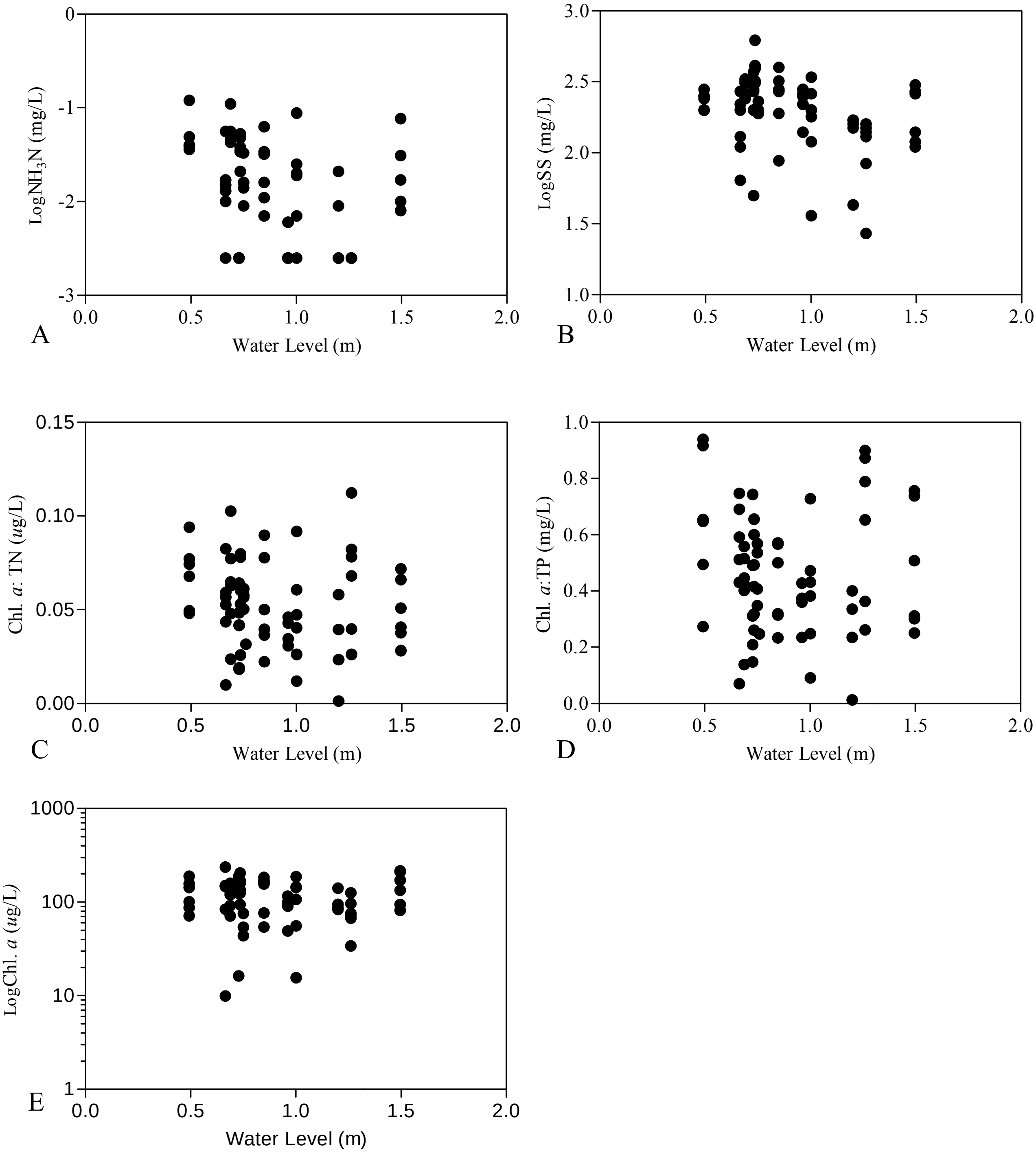


Figure 2.14 Relationships between water level and monthly water quality data collected in 2009: A) Ammonia nitrogen, B) Suspended solids. C) Chlorophyll *a*:TN ratio. D) Chlorophyll *a*:TP ratio, E) Chlorophyll *a*.

2.5 Discussion

Lake Ellesmere/Te Waihora has undergone many changes in water quality since its formation 3000 years ago, from being a major discharge point for the Waimakariri River, to a tidal estuary, to a freshwater lake and today a brackish lake. Currently, the lake has severely degraded water quality, particularly indicated by the presence of high nutrient concentrations, high algal biomass and poor water clarity throughout the lake. Although, total lake nitrogen concentrations have significantly decreased over the last 15 years, dissolved phosphorus concentrations have significantly increased (Hayward & Ward 2009). Reductions in total nitrogen concentrations have been primarily attributed to decreased dissolved inorganic nitrogen loading from inflowing tributaries and improved farm management (Hayward & Ward 2009). However, the significant increase in DRP is in contrast to a decrease in phosphorus loadings from tributaries (Hayward & Ward 2009). Change in water level (primarily related to opening regime) was not found to influence nutrient concentrations, except for ammonia nitrogen, which was lower at intermediate lake levels and higher at both low and high water levels. Furthermore, a positive relationship was observed between chlorophyll a (related to reduced clarity) and salinity. Although the lake is primarily opened to reduce flooding, some studies have shown improvements in water quality and phytoplankton biomass when the opening is greater than one month, however there is not yet enough data to quantify this (Schallenberg *et al.,* 2010). My results suggest lake opening events are not effective at improving water quality or reducing phytoplankton biomass in Lake Ellesmere/Te Waihora (Figure 2.14).

2.5.1 Water quality and the role of nutrient dynamics

Kaituna Lagoon at the eastern end of the lake generally had the highest overall water quality, with lower suspended solids, nutrients and chlorophyll a concentrations (Figures 2.3, 2.4 and 2.8). This is indicative of low nutrient inputs from eastern catchments, including the Kaituna River (Hayward & Ward 2009). However, low dissolved oxygen concentrations were recorded in Kaituna Lagoon throughout the year, a condition that may be related to an increased demand for oxygen from microbial/bacterial respiration in bottom sediments and slower re-aeration rates in the sheltered area (Ward *et al.,* 1996). Greenpark Sands was the most similar site to Kaituna Lagoon, although nutrient concentrations were much higher (Figure 2.4 and 2.6). High phosphorus concentrations may be related to high phosphorus loading from the Halswell river and LII river (Hayward & Ward 2009). The four long-term monitoring sites (Selwyn Huts, Timberyard, Mid Lake and Taumutu) were all similar in water quality, but the poorest water quality was the Mid Lake site, possibly due to lower dilution and mixing with freshwater from tributary inflows. In comparison to three other coastal brackish lakes in Canterbury; Forsyth/Wairewa, Coopers Lagoon/Muriwai and Wainono Lagoon, Lake Ellesmere generally had similar total nitrogen and phosphorus concentrations (with the exception of Coopers), but had elevated chlorophyll a concentrations. Lake Ellesmere/Te Waihora and Forsyth/Wairewa generally had the most similar water chemistry conditions with mid brackish salinities (5 – 9 ppt) compared to Coopers Lagoon/Muriwai and Wainono Lagoon which had much lower chlorophyll *a* concentrations and salinity (0-3 ppt).

High suspended solids concentration in the water column decreases water clarity and light penetration, which can limit phytoplankton growth (Schallenberg *et al.,* 2010). High suspended solids concentrations in the lake, reflects its shallow depth and constant re-suspension of bed sediments through wind and wave forces (Sagar *et al*., 2004; Jellyman *et al*., 2009). Re-suspension of bed sediments in the lake is further increased by lack of macrophyte beds, which would help provide stabilisation of bottom sediments and reduce wave action (Scheffer 2001). A feasibility study on the potential to re-establish macrophyte beds in Lake Ellesmere/Te Waihora identified light limitation and wave induced water level turbulence to be the dominant driving forces preventing macrophyte establishment in the lake (Sagar *et al.,* 2004). However, other factors such as salinity and grazing pressure by birds are also likely important. Unstable soft sediments are likely to increase the sensitivity to uprooting by animals and waves (Sager *et al*., 2004). Shallow brackish lakes are usually turbid (Scheffer 2001) and interestingly, they can be densely vegetated at the same time (Bales *et al*. 1993; Jeppesen *et a*l., 1994; Moss 1994). However, the connection between high water clarity and submerged vegetation characteristic of freshwater lakes has not been found in brackish systems (Jeppesen *et al.,* 1997). Water clarity periodically improved during periods of stable weather when fine sediments settled out of suspension (visual observation). However, periods of stable weather at Lake Ellesmere/Te Waihora are relatively infrequent, due to the exposure of the lake to coastal winds. During periods of calm, warm weather, when suspended inorganic sediment concentration is often low, increased water clarity and light penetration may promote phytoplankton growth (Hawes & Ward 1996; Hamilton 2008), which may subsequently decrease water clarity. However, should a calm period coincide with a phytoplankton bloom decay, there is potential for lake water to become anoxic as oxygen consumption exceeds photosynthetic replacement (characteristic of most hypertrophic lakes; Scheffer 2001).

The seasonal dynamics of nutrient availability in shallow lakes are complex. As with other shallow lakes the high relative sediment-water contact from wind-induced turbulence ensures a rapid return of material into the water column (Hamilton & Mitchell 1997; Schallenberg & Burns 2004). In addition, relatively high temperatures in summer lead to an increase in mineralisation rates, and consequently to a further release of nutrients from the sediment (Jeppesen *et al.,* 1997). The higher sediment-water contact gives an extra dimension to the eutrophication problem, as much of the phosphorus historically absorbed by the sediment during eutrophication may be re-released to the water column. This is often referred to as 'internal nutrient loading' and can cause a delay of many years in the response of lake water concentrations to a reduction of external loading. The dynamics of nitrogen within shallow lakes have been less well studied. However, the sediment buffer effect seems to be less relevant for nitrogen (Jensen *et al.,* 1991). Instead substantial amounts of nitrogen have been shown to disappear from shallow lakes as a result of denitrification (Jensen *et al.* 1991). Denitrification is the process whereby nitrate is microbially transformed into N_2, which cannot be used as a nutrient by most algae (compared with several cyanobacterial species) and largely diffuses as gas to the atmosphere (Scheffer 2001).

The predominant forms of nitrogen and phosphorus present in Lake Ellesmere/Te Waihora are organic (Figure 2.3C and 2.6B). This reflects the processes by which mineralised nutrient forms are rapidly taken up by plant growth. In Lake Ellesmere/Te Waihora uptake is almost entirely into algal cell material (phytoplankton) (Larned & Schallenberg 2006). Concentrations of inorganic nitrogen and phosphorus were highly variable throughout the lake and varied seasonally, generally peaking over late summer months (February to March; Figure 2.5B and 2.7B). Summer peaks are likely related to periods of high algal blooms and increased mineralisation rates in the sediments and inputs from inflowing streams. A slight decrease in nutrients was observed at higher water levels in winter and was mostly likely related to increased dilution and/or lower temperatures reducing internal nutrient cycling processes. However, in general increased tributary inputs keep dissolved nutrient concentrations elevated over winter, particularly nitrate + nitrite nitrogen concentrations. This is a feature of the catchment's groundwater system, which shows seasonal peaks in nitrate load from spring-fed streams (Hughey & Taylor 2009). Estimates of annual inputs of total phosphorus into the lake, indicate that the single largest load comes from the Selwyn River which carries sediment from the upper catchment when in flood (Larned & Schallenberg 2006). Reducing external nutrient loads from the catchment would undoubtedly be beneficial for lake health in the long-term. This may be achieved through such activities as improving riparian planting or wetland systems surrounding the lake to help process nutrients before they enter it, improving fencing along tributary and lake margins to keep stock out, and reducing shoreline erosion, thereby reducing sediment inputs to the lake. Additionally, improving farm management techniques (nutrient budgeting and stocking rates) will help reduce the risk of nutrient loss. While reducing nutrient loading to some lakes has resulted in improved trophic status (Jeppesen *et al*., 2007), improvements in shallow lakes can take years, due to high internal nutrient cycling and other ecological feedbacks (Jeppesen *et al.,* 2007).

2.5.2 Phytoplankton relationship with nutrients

Lake Ellesmere/Te Waihora experienced high chlorophyll a concentrations throughout the year, generally reflecting year round high phytoplankton production. Chlorophyll *a* concentrations were positively related to total nitrogen and phosphorus concentrations in the lake (Figure 2.9) and with lower water clarity (Figure 2.9). In some shallow lake systems with high sediment re-suspension, chlorophyll a concentrations may also reflect chlorophyll a from re-suspended epiphytic (benthic) algae (Hakanson *et al*., 2007). However, due to light limitation in Lake Ellesmere/Te Waihora (Hawes & Ward 1996), epiphytic algae are likely to contribute little to chlorophyll *a* concentration. Chlorophyll *a* concentrations were relatively high at all lake sites, except in Kaituna Lagoon where they were lower contributing to improved water quality conditions.

Generally, a major part of the total amount of phosphorus in the water column over summer in shallow lakes is contained in algal cells (Scheffer 2001). Some phytoplankton species control buoyancy to maintain position in the water column, thus maintaining their cellular phosphorus in suspension (Scheffer 2001). Larned & Schallenberg (2006) suggested that the water quality conditions in Lake Ellesmere/Te Waihora favour the growth of these phytoplankton taxa. Unfortunately, some of these taxa are undesirable, bloom forming taxa, including *Microcystis aeruginosa* and *Anabaena* sp., both of which and have been recorded in abundance over summer in the lake (Ecan unpublished data). It is therefore, not surprising that total phosphorus concentrations peak in summer and were positively related to chlorophyll *a* concentrations in the lake (Figure 2.7B & 2.9B). There is debate in the scientific community as to the interpretation of causality with respect to such correlations, as algae stimulate release of sediment bound phosphorus into the water column. Thus, to some extent, algal biomass may explain total phosphorus concentrations rather than vice versa. I suspect there is a positive feedback loop-effect in the lake, such that the originally high nutrient input into the lake allowed prolific algal biomass to accumulate. Subsequently, excess nutrient inputs have been bound up in sediments, but are being re-mineralised back into the water column by bacteria.

2.5.3 Influence of water level fluctuations

Water level fluctuation was related to many physical and chemical properties in the lake, such as the observed temperature difference across the littoral zone around the lake and fluctuating salinity. Biota in the eulittoral zone would have experienced harsher extremes of temperature than biota in the mid-littoral and lower littoral zones due to dewatering. This suggests the eulittoral zone experiences desiccation before the mid-littoral and lower littoral zone and shallower water in the eulittoral zone offers less buffering of temperature changes than deeper water. Lower water levels (during summer and lake openings) were also significantly related to higher concentrations of ammonia nitrogen (due to dilution concentrations effect) and total suspended solid concentration. Similarly, temperature (Figure 2.10) and dissolved oxygen (*Wilks unpubished)* concentrations decreased at lower water levels, suggesting water quality in Lake Ellesmere/Te Waihora may be improved by higher water levels.

Salinity in the lake increased as the frequency and duration of lake opening events increased (Figure 2.12) and was significantly related to water level (Figure 2.13). There were short term, and often dramatic fluctuations in salinity near the lake opening/sea barrier and more damped, whole lake variations in the longer term (> 5 days), suggesting a lag before salinity increase around the whole lake. Salinity concentraions are mainly dependent on how long the lake outlet is open and how much seawater enters (Larned & Schallenberg). This factor in turn is dependent on the lake level, tidal cycle and sea conditions (Horrell 2008; Spigel 2009).

Salinity was found to be significantly positively related to chlorophyll *a* concentration, which has not previously been reported in Lake Ellesmere/Te Waihora. This is in contrast to Schallenberg *et al.* (2010), which analysed a larger data set of water quality parameters from lake Ellesmere/Te Waihora (1992-2007) and reported a slightly positive, but not significant relationship between chlorophyll *a* and salinity. Research on hypersaline lakes has often shown high phytoplankton chlorophyll *a* levels (Hammer & Hestline 1988) and higher rates of primary production than those reported in eutrophic freshwater lakes (Wetzel 1983). It has been suggested that the causal factor in this relationship is a change in zooplankton community structure and the release of phytoplankton from grazing pressure (Scheffer 2001). Grazing pressure from the dominant zooplankton species in Lake Ellesmere/Te Waihora, (calanoid copepods), is reportedly relatively minor (Larned & Schallenberg 2006) and is unlikely to explain the increase in phytoplankton density at higher salinities. Perhaps zooplankton composition in the lake is structured by salinity, which if reduced could allow other zooplankton species to establish and exert more control over phytoplankton. In contrast to copepods, cladocerans such as *Daphnia* are more efficient filter feeders and are capable of reducing phytoplankton biomass (Scheffer 2001). However, *Daphnia* species are sensitive to high inorganic turbidity (Jack *et* al., 1993), saline concentrations (Schallenberg *et al.,* 2003) and not all cladocerans would have the same impact on phytoplankton biomass as *Daphnia*. Therefore, current water quality conditions are unfavourable for *Daphnia* populations. If the lake was to become less brackish by increasing mean lake level, and less turbid, *Daphnia* could potentially establish and reduce phytoplankton biomass in the lake, significantly.

A recent study on the relationship between chlorophyll *a*, nutrients and salinity across a range of lakes from freshwater to marine, found a significant salinity threshold. Håkanson & Eklund (2010) reported a minimum chla: TP ratio, in the salinity range 2 -5 ppt, followed by an increase up to a salinity of 10 -15 ppt, and then a continuous reduction at higher salinities. Similarly, in New Zealand, Schallenberg *et al.,* (2010) found that chlorophyll *a* concentration fell in Waituna Lagoon as salinity increased from 2 ppt to 35 ppt. However, the study of Schallenberg *et al.* (2010) was related to lake opening events and successful flushing of nutrients. Håkanson & Eklund (2010) suggest a salinity threshold of ~ 10 ppt, beyond which chlorophyll a concentrations generally decrease, possibly due to physiological effects on the function of phytoplankton cells and/or to salinity influencing the distribution between bioavailable (dissolved) fractions of nitrogen and phosphorus, so that less of the nutrients appear in dissolved forms at higher salinities. Schallenberg *et al.* (2010) suggested that Lake Ellesmere/Te Waihora would have to be open to the sea for ~200 days for salinity in the rest of the lake to approach that of sea water. However, they suggested that artificially extending the opening period could have several negative effects. This could be particularly on fringing vegetation, due to water level reduction (Johnson & Partridge 1998), and on lake biota, by increasing salinity beyond their tolerance limits (Schallenberg *et al*. 2003). It is likely that the observed relationship between chlorophyll a and salinity in Lake Ellesmere/Te Waihora is related to the amount of readily available dissolved nitrogen and phosphorus. It is likely that when the lake is opened, nutrients bound to sediments are re-suspended into the water column, creating a new pulse of readily available nutrients, thus stimulating phytoplankton growth. In the absence of potentially negative effects, it would be interesting to see whether increased/extended salt water intrusion, and thus whether increased lake salinity, would decrease phytoplankton biomass in the Lake Ellesmere/Te Waihora. In the short-term, effort needs to be focused on reducing nutrient loads to the lake and thus exerting increased nutrient limitation on phytoplankton.

2.5.4 Implications for management

It is well established that internal lake processes are complex. Due to the readily available nutrient supply in Lake Ellesmere/Te Waihora, increased water clarity or light availability via stabilisation of sediments will coincide with a negative response, such as an algal bloom. The water quality in Lake Ellesmere/Te Waihora is poor, with high nutrients, high phytoplankton production and poor water clarity. Although the lake has shown signs of improvements, such as reduced total nitrogen concentrations, many other water quality parameters are increasing and the lake is starting to experience an increased frequency of persistent toxic algal blooms.

Many interest groups have expressed a desire to re-establish macrophytes in the lake, in the hope that they will improve water clarity, stabilise bottom sediments and increase biological diversity. However, conditions in the lake for re-establishment are unfavourable for macrophytes and even if habitat for macrophytes were restored in the lake, Jellyman *et al*., (2009) suggest that more frequent occurrences of nuisance blue-green cyanophyte blooms would be likely, and salinity would likely restrict a number of plants to areas of freshwater inflows. Thus, there needs to be careful consideration as to the best approach to reducing further lake degradation and improving water quality. A higher water level, together with a reduction in nutrient loading through improved riparian vegetation, fencing of tributaries and lake margins and improved farm management, are among the first steps to improving water quality.

Chapter 3

Lake level fluctuation and the response of benthic fauna

3.1 Abstract

Lake Ellesmere/Te Waihora is a shallow, hypertrophic, brackish lake in Canterbury, New Zealand, that regularly experiences fluctuations in water level. The effects of water level fluctuations on benthic invertebrate communities in the littoral zone were investigated. Taxonomic richness and density were significantly higher in the eulittoral zone compared to the mid-littoral and lower littoral zones and varied spatially around the lake. Crustacea (*Paracorophium excavatum*), Oligochaeta, Mollusca (*Potamopyrgus antipodarum*) and Chironomidae (*Chironomus zealandicus*) were dominant community members, although 24 other taxa were also collected. At higher water levels, taxonomic richness increased in the eulittoral zone, while decreasing in the mid-littoral and lower littoral zones. In contrast, density decreased with higher water level in the eulittoral and mid-littoral zones, while increasing in the lower littoral zone. My results suggest that the eulittoral zone is the most diverse and productive zone in Lake Ellesmere/Te Waihora. However, it is also the most at risk to dewatering, high temperatures, desiccation and loss of habitat. The current lake opening regime is favourable to benthic invertebrate survival as the lake is predominantly open over winter when temperatures are lower, reducing the risk of desiccation. This research indicates that lake level is a major driver of the ecology of the littoral zone of Lake Ellesmere/Te Waihora, and although lake openings generally occur during winter months, care should be taken to ensure extreme reduction in lake levels do not occur during summer. Based on results from this study, I suggest a minimum lake level at Taumutu of 0.6 m during the months from November – April in order to protect benthic invertebrate communities in the eulittoral zone from extensive loss of habitat, extreme temperature and reduced risk of desiccation.

3.2 Introduction

The littoral zone is probably the most dynamic zone within a lake ecosystem. It is the interface between the terrestrial environment and open water, receiving, processing and modifying inputs from river mouths and the surrounding catchment (Scheffer 2001; Kelly & McDowall 2004; Free *et al*., 2009). This dynamic ecotone is characterised by highly variable physical conditions and strong wind and wave action (Verschuren *et al.,* 2000; Aroviita & Hämäläinen 2008). The littoral zone is frequently a region of high biodiversity and productivity, and organisms that live in it may have to cope with oscillating water velocities, shear stress and turbulence associated with water level and temperature fluctuations (Benson & Hudson 1975; James *et al*., 1998; Scheifhacken *et al.,* 2007; de Mendoza & Catalan 2010). Benthic invertebrates constitute a significant biomass and play an important role in overall production in lake ecosystems (James *et al.,* 1998; Free *et al*., 2009). In Lake Ellesmere/Te Waihora, the littoral zone covers a considerable area of the lake and processes affecting this zone probably have a strong influence on the ecology and productivity of the whole lake. In Lake Ellesmere/Te Waihora the littoral zone is continually expanding and contracting due to fluctuating water levels driven by wind and wave forces and manual opening events. Fluctuating water levels can create a number of pressures on benthic invertebrates, from desiccation to decreases in habitat availability and food resources (James *et al.,* 1988). However, implications and precise effects of water level changes on littoral zone and aquatic communities in Lake Ellesmere/Te Waihora are relatively unknown.

3.2.1 Littoral zone

A typical lake has three distinct zones: littoral, pelagic, and benthic (Wetzel 1983). The littoral zone is the near-shore area where sunlight penetrates all the way to the sediment and allows aquatic plants (macrophytes) to grow. The pelagic zone is the open water area where light does not penetrate to the bottom. The benthic zone, is the bottom of the lake. There is considerable interaction between biota that use the littoral zone and pelagic zone, with many species using both zones at various stages in their life histories. For example, larvae utalise and adults of fish species, such as koaro (*Galaxias brevipinnis*), spawn in the recently inundated shallow littoral zone (Rowe *et al.,* 2002). The macroinvertebrate fauna of the littoral zone is generally the most diverse component of the fauna in lakes (Biggs & Malthus 1982; James *et al*., 1998). Invertebrate fauna in New Zealand lakes is generally less diverse than overseas lake ecosystems with several taxonomic groups poorly represented or absent (Winterbourn & Lewis 1975; Mylechreest 1978; Forsyth 1987; Sanders 1994; Kelly & MacDowall 2004). However, a number of insect groups (e.g. chironomids, dragonflies and damselflies), annelids, crustaceans and mites can be abundant (Timms 1982; James *et al*., 1998).

The littoral zone can be further divided based on vertical gradients, which have been described by several workers (Pearsall 1920; Segal 1971). However, a more descriptive classification of distinctive zones within the littoral zone has been proposed by Kelly & McDowall (2004). These workers sub-divided the littoral zones of deep macrophyte-dominated lakes in New Zealand into four sub-zones: eulittoral, upper littoral, middle littoral and lower littoral. The littoral zone of shallow turbid lakes (< 10 m deeep) is less well documented than that of macrophyte-dominated lakes. However, the littoral zone in shallow turbid lakes probably has at least three distinct zones based on general shallow lake morphology (Scheffer 2001): eulittoral zone, mid-littoral zone and lower littoral zone.

These subzones are based on physical attributes, such as wave exposure, substrate composition, and life supporting parameters, with each zone having a somewhat distinct biotic community (Kelly & McDowall 2004). Gradients in these physical and biological attributes provide high heterogeneity of conditions for invertebrates and fish (Weatherhead & James 2001; Takamura *et al.,* 2009). Differences in substrate composition in the littoral zone (e.g., cobles, sand, silt, macrophyte or woody debris) are considered the most important factors determining macro-invertebrate community composition and abundance (James *et al.,* 1998; Verschuren *et al.,* 2000; Tolonen *et al.,* 2001; Weatherhead & James *et al*., 2001; Free *et al.,* 2009; Takamura *et al.,* 2009). For example, macrophytes have been shown to develop a unique macroinvertebrate fauna in littoral areas compared to other substrate such as silt or sand (Tolonen *et al*., 2001). The species of macrophyte and their biomass can also greatly influence taxonomic richness and abundance of macroinvertebrates (Hanson 1990; Strayer *et al*., 2003; Kelly & Hawes 2005). Several other factors that influence macroinvertebrate community structure in the littoral zone are wind exposure (Allan & Kirk 2000), cyanobacterial blooms (Oberholster *et al.,* 2009) dissolved oxygen concentration and nutrient levels (Free 2009), water depth and fluctuating water levels (Kato *et al.,* 1990; Frazer *et al*., 1998; Thompson & Ryder 2008; McEwen & Butler 2010). Fish have also been shown to affect macroinvertebrate community structure in the littoral zone, both directly through predation (Keast & Harker 1977; Diehl 1992; Naestat & Brittain 2010; Nurminmen *et al.,* 2010) and indirectly through habitat disturbance (Moore 2006). Toxic cyanobacterial blooms (a consequence of eutrophication) have also been shown to influence macroinvertebrate community composition in the littoral zone. Oberholster *et al.,* (2009) found an increase in macroinvertebrate abundance but reduced diversity at sites dominated by a cyanobacterial bloom compared to sites not impacted by the bloom, which had higher diversity but lower abundance. Benthic invertebrates play a key role in the littoral zone of lakes as they potentially control the biomass of periphytic algae (Hawes & Schwarz, 1996; James *et al*., 2000), recycle detrital material (Kornijów *et al*., 1995) and provide a critical link from primary production through to higher trophic organisms, such as fish (Graynoth *et al*., 1987; Graynoth & Jellyman 2002).

3.2.2 Pressures on lake ecosystems

Lake ecosystems are particularly susceptible to impacts from human activities such as agriculture, urbanisation and water level manipulation (Carpenter *et al*., 1998; Søndergaard & Jeppesen *et al.,* 2007; Della Bella & Mancini 2009; Donohue *et al*., 2009; Glaz *et al*., 2009). Of these, agricultural activities resulting in eutrophication (elevated nutrients) are one of the most common water quality problems in lakes, worldwide (Vadeboncoeur *et al*., 2003). Shallow lakes in particular are more at risk from eutrophication, as there is a larger interface between the surface layer and lake bed than in larger lakes and, therefore, substances and processes in sediments can influence the water column to a much greater extent (Schallenberg & Burns 2004; Qin *et al.,* 2007). In many countries, reducing external nutrient loading has become the main focus for lake managers (Søndergaard *et al.,* 2007). Despite the increase in land use pressures on lake ecosystems, comparatively little research in New Zealand has tested the impacts of various forms of disturbance and their impact on littoral zones. In New Zealand, much limnological research has been conducted on macrophytes (Stark 1981; Biggs & Malthus 1982; Hawes *et al.,* 2003; Kelly & Hawes 2005; Bickel & Closs 2008), benthic invertebrate community structure and fish (Ward *et al.,* 2005; Wissinger *et al.,* 2006; Kelly & Jellyman 2007) particularly, in the shallow littoral of deep lakes (Myclechreest 1978; Stark 1981; James *et al*., 1991; Sanders 1994; Weatherhead & James 2001; Thompson & Ryder 2008). However, few studies in New Zealand have investigated benthic community distribution along the littoral zone (Weatherhead & James 1998). This has been partially due to the difficulty in sampling macrophytes (which often dominate littoral zones) and large variations in replicate samples (James *et al*., 1998; Baumgärtner *et al*., 2008). Early studies described general patterns in invertebrate community structure associated with macrophyte distribution (Winterbourn & Lewis 1975; Biggs & Malthus 1982; Kirk & Henriques 1986) and seasonal changes in invertebrate abundance associated with macrophytes (Mylechreest 1978). A clear relationship between the presence of macrophytes and invertebrate abundance and diversity has been shown from these studies, but there have been few attempts to relate invertebrate distribution to physical parameters such as water level fluctuations in New Zealand.

3.2.3 Water level fluctuations

Water level fluctuations are important processes contributing to the dynamic nature of the littoral zone (Fernández-Aláez *et al.,* 1999; Hofmann *et al.,* 2008; Keto *et al.,* 2008; Wantzen *et al.,* 2008). Time scales of water level fluctuations can range from seconds to days, and have the potential to drive benthic invertebrate abundance and composition (Hofmann *et al*., 2008). Short-term water level fluctuations (seconds to hours), impose relatively minor physical stress on organisms living in the littoral zone and are generally driven by wind or boat waves and result in a small changes in water level. In contrast, long-term water level fluctuations (days – years) driven by lake level management, may place considerable stress on benthic invertebrates by changing habitat availability and exposing them to extreme environmental conditions. Furthermore, anthropogenic disturbances (e.g. water abstraction for irrigation) can alter natural hydrologic cycles causing water level fluctuations that can surpass the physiological or behavioural adaptability of many organisms (Coops *et al*., 2003; Cott *et al*., 2008). In Europe and North America a number of studies have assessed the effect of natural (e.g., wind, waves and climatic variables) and man-made water level fluctuations (e.g. lake level management, power generation) (Fernández-Aláez *et al.,* 1999; Hofmann *et al.,* 2008; Keto *et al.,* 2008; Wantzen *et al.,* 2008). They include studies on the distribution and response of macrophytes (Rørslett 1984 & 1989), phytoplankton and zooplankton (Turner *et al.,* 2005; Heinsalu *et al*., 2008), macroinvertebrates (Chow-Frazer *et al.,* 1998; White *et al*., 2008), fish (Fischer & Uta Ohi 2005; Sutela & Vehanen 2008), and birds (Romano *et al*., 2005; Takekawa *et al.,* 2006; Timmermans *et al*., 2008. For example, extensive dewatering of the littoral zone as observed in reservoirs, negatively affects benthic invertebrate abundance by decreasing available habitat and those organisms that cannot migrate or withstand periods of desiccation might be lost from the system (Currier 1954; Fisher & LaVoy 1972; Hunt & Jones 1972; Trotzky & Gregory 1974; McAfee 1980; Blinn *et a*l., 1995; Prus *et al.*, 1999; Richardson *et al*., 2002). Furthermore, reduced water levels can stress littoral invertebrates by desiccating or freezing littoral sediments and vegetation (Coops *et al*., 2003), which often results in a shift in the littoral community along the littoral zone gradient where hardier species often become the new dominant species (Hudon 1997; McGowan *et al*., 2005). A number of studies have found a variable response of lake biota to the frequency, duration and extent of water levels change. More extreme fluctuations tend to have the most detrimental effects on lake biota, whereas small, short term fluctuations in water level can be beneficial (Pinay *et al*., 1990; Richardson *et al*., 2002). For example, periodic flooding has been shown to be important for retaining and replenishing nutrients and other materials that contribute to the development of riparian plant communities (Pinay *et al*., 1990). However, persistently elevated water levels can lead to defoliation of riparian vegetation, eventually causing a shift in the type of vegetation present (Hudon 1997), and induce a cascade of effects on organisms dependent on the previous plant community (terrestrial and aquatic) (McGowan *et al.,* 2005). In contrast, extensive dewatering can have significant impacts on the survival of aquatic invertebrates, as they often depend on specific types of aquatic vegetation for food, shelter and egg deposition, and any shift in the vegetation community can cause a drastic reduction of the invertebrate population (Hunt & Jones, 1972). For example, larvae of some aquatic insects require emergent vegetation to complete metamorphosis from larva to adult (Thorp & Covich 1991). During metamorphosis, insects such as mayflies, dragonflies, and damselflies, may use emergent vegetation to rest on while they moult and emerge as adults (Thorp & Covich 1991). If water levels are markedly lower than normal, emergent macrophytes can die or dry out, reducing available substrate and therefore opportunities for many invertebrates to emerge and complete their life cycles. Water level fluctuations associated with lake level management and dams can also influence and alter biogeochemical processes in lakes. In particular, flooding can extend into the littoral zone, inundating vegetation, resulting in releases of methane gas (Juutinen *et al*., 2001). Flooding can also physically alter riparian areas by scouring banks, cutting new channels, and by redistributing organic matter and sediments (Rosenberg *et al*., 1987; Bonetto *et al*., 1989). Impacts, such as these, can change the concentration of dissolved organic carbon, which affects numerous biogeochemical processes that control water quality (e.g., bioavailability of contaminants, and nutrient cycling), in addition to altering light penetration into aquatic systems (Prowse *et al*., 2001).

3.2.4 Research context

The littoral zone of a lake is a region of high biodiversity and productivity. In Lake Ellesmere/Te Waihora the littoral zone is continually expanding and contracting due to fluctuating water levels driven by wind, wave forces and manual lake opening events. Implications for water advance/recession in the littoral zone, and the ways that aquatic communities respond, are relatively unknown. Therefore, in this study, I examined the effects of fluctuating water levels on littoral benthic invertebrates at three depths along the littoral zone gradient. I compared taxonomic richness, density and composition of invertebrate assemblages between three seasons and differing water levels. I hypothesised that community composition would be impacted by water level fluctuations, and be greater in the eulittoral zone than the deeper lower littoral zone. Specifically, I addressed the following questions:

1. Do benthic invertebrate communities differ between the eulittoral, mid-littoral and lower littoral zones?
2. Are there spatial differences around the lake in benthic invertebrate richness and community composition in the littoral zone?
3. Do benthic invertebrate communities change seasonally?
4. What environmental factors have the most influence on littoral benthic invertebrate communities?

3.3 Methods

3.3.1 Study site

The shallow windswept nature of Lake Ellesmere/Te Waihora creates a fluctuating littoral zone. In order to quantify the effects of lake level fluctuations on the benthic invertebrate community of the littoral zone, I established sampling transects at five locations around the lake; Kaituna Lagoon, Greenpark Sands, Selwyn Huts, Timberyard and Taumutu (Figure 3.1). The littoral sediment varied around the lake, but consisted primarily of silty sands and small cobbles (Wood 2008).

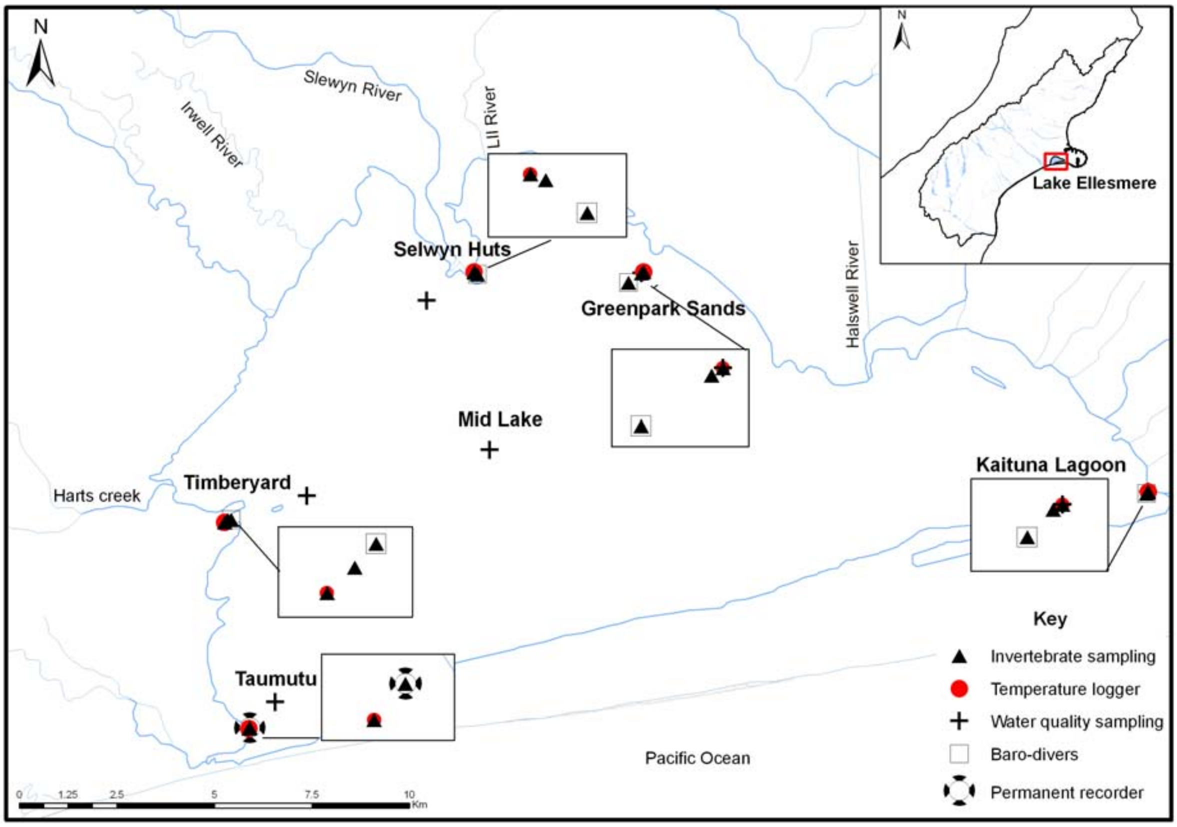


Figure 3.1 Sampling locations and sub-littoral sites around Lake Ellesmere/Te Waihora.

3.3.2 Water quality parameters

A number of water quality parameters were measured monthly at five sites from January – December 2009 (Figure 3.1). Parameters included total suspended solids, nitrogen and phosphorus concentration in their particulate/organic and dissolved forms, and chlorophyll a concentration. At each site, dissolved oxygen, temperature and salinity were measured using a hand held meter (Pro DOPTO Model 3100 and YSI 30). Depth was measured at each site and vertical water clarity was estimated with a secchi disc. Samples were generally collected between early morning and mid day (9 am – 1 pm).

3.3.3 Water level measurements

A permanent water level recorder (mean sea level) maintained by Environment Canterbury has been operational at Taumutu (near the lake outlet) since March 1994. In order to gain a better understanding of spatial water level fluctuations, four barometric divers (Baro-diver SN 26383) were installed in April 2009. Loggers were installed at lower littoral sampling locations at Kaituna Lagoon, Greenpark Sands, Selwyn Huts and Timberyard (Figure 3.1 & 3.2). The lower littoral zone was expected to remain under water. However, low water levels (~ 0.08 m) at Kaituna Lagoon were reduced to below placement of barometric-divers (0.10 m above substrate) and resulted in lower than recorded water levels (Appendix 2). Barometric divers recorded water level at 15 minute intervals by registering changes in pressure, and were downloaded 3 monthly until final collection in January 2010. Advice given from hydrology and groundwater staff at Environment Canterbury suggested barometric-divers would give a comparative indication of water level and change as the permanent recorder.

Spot water level recordings made throughout 2009 were compared with barometric-diver recordings and there was an overall average difference of 15.4 mm (Table 3.1). Using barometric data, ground truthing and visual observations I was able to calculate an average water level at each site. When lake level dropped below this value, dewatering most likely occurred in the eulittoral zone (Table 3.1).

Table 3.1 Mean difference in water level between observed measurements and recorders.

	n	Mean diff (m)	SE	Eulittoral Dry water level (m)
Kaituna	4	0.049	0.018	< 0.1
Greenpark	4	0.026	0.009	< 0.18
Selwyn	4	-0.009	0.006	< 0.08
Timberyard	4	0.003	0.002	< 0.15
Taumutu	8	0.013	0.007	< 0.5
Overall	24	0.015	0.006	< 0.6

3.3.4 Sampling design

Benthic invertebrates were initially sampled in January (summer) 2009, when the lake had been closed for 4 months (mean water level 0.75 m), in May (autumn) 2009 when lake level was high (mean water level 1.27 m), and again in August (winter) 2009 after the lake had been manually opened and naturally closed 5 times over the preceding 3 months (mean water level 0.52 m). Invertebrate data collected in May (autumn) 2009 from the eulittoral zone at Greenpark Sands was excluded from the data set and all statistical analyses, due to high water levels and a large shift in the eulittoral sampling location (1 km). Furthermore, all May results were excluded from analyses, unless specifically stated in results, due to high water levels. Only representative samples from the eulittoral zone were able to be collected. At each of the five sampling locations (Kaituna Lagoon, Greenpark Sands, Selwyn Huts, Timberyard and Taumutu), a transect perpendicular to the lake edge was established (Figure 3.1 & 3.2). This transect consisted of a gradient of three sites from the eulittoral lake shore out into the lower littoral zone (Figure 3.2). The lower littoral zone was located at a depth that was expected to remain under water for most of the year. The length of the transect varied with location and lake bed gradient, but ranged from 20 m at Taumutu to 1.2 km at Greenpark Sands.

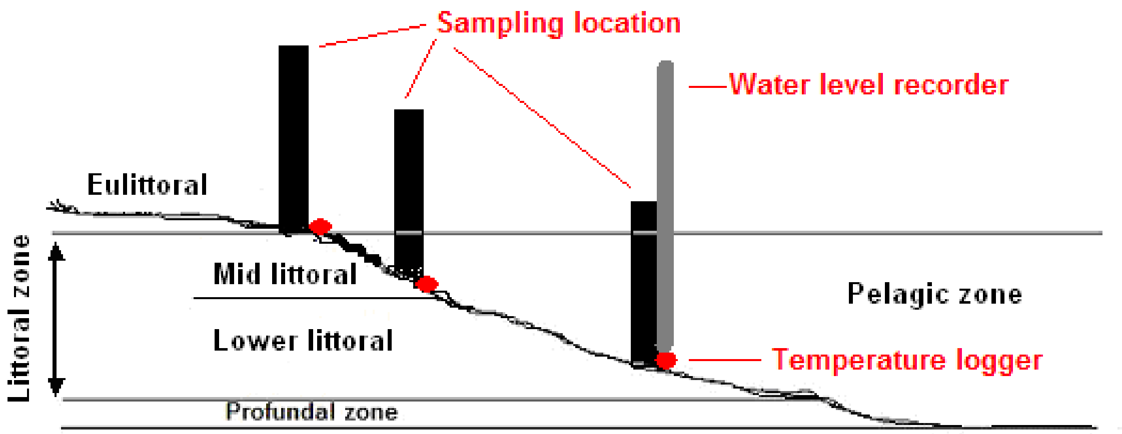


Figure 3.2 Location of sampling sites along the littoral zone gradient.

3.3.5 Invertebrates

Benthic invertebrates were sampled quantitatively using a Hess sampler (320 mm diameter, 200 μm mesh) on three occasions at three different depths in the littoral zone over the course of 2009. Three replicate samples were taken at each of the three sites along the longitudinal gradient (e.g. eulittoral, mid-littoral and lower littoral sites). The exception to this was at Taumutu where only two sites (eulittoral and mid-littoral) were established and sampled due to shore gradient, depth and personal safety. The Hess sampler was placed into the lake bottom substrate and the top ~0.01 m of substrate was stirred for 1 minute. In winter, when the lake level was low and the eulittoral substrate was damp (but not covered by water), a sample of ~0.01 m of substrate was collected and filtered through a 200 μm mesh in the field. All samples were preserved in 90% ethanol in the field. In the laboratory, large samples were sub-sampled using a barrel splitter and then strained through a 200μm sieve. All invertebrates were identified using a dissection microscope (magnification 10 x) to the lowest taxonomic level possible according to keys in Winterbourn *et al.,* (2008) and Chapman & Lewis (1976). In some cases this was to species level, but for some taxonomic groups identification was only to phylum (Nematoda) or class (Oligochaeta and Copepoda).

3.3.6 Data analysis

Both multivariate and univariate methods were used to analyse the data (Reynoldson *et al.,* 1997). One-way analysis of variance (ANOVA) with Tukey's multiple comparison tests (Tukey's test), were used to test for differences between sites and linear regressions were used to look at the relationship between individual environmental variables and benthic invertebrate composition. Data were transformed where necessary. Values were considered significant when $P < 0.05$. Multidimensional scaling (MDS) ordinations, and Analysis of Similarities (ANOSIM) were used to test for differences between benthic invertebrate community composition at the eulittoral, mid-littoral and lower littoral sites. MDS was performed on square-root transformed relative densities (individuals m^{-2}) of benthic invertebrates. A red dotted elipse was drawn onto MDS graph to help draw attention to groupings. Square root transformation was used as it results in medium down-weighting of common species and allows for a good discrimination of sampling sites (Clarke & Warwick 2001).

In order to relate invertebrate data and environmental data in sub-littoral zones, Redundancy Analysis (RDA), with Monte Carlo permutation tests for significance, was applied (Lepš & Šmilauer 2003). Before all analyses the invertebrate density data were checked for normality and square root transformed, water quality data were log transformed (x+1) to stabilise variances and rare taxa (n < 4) where removed. Ten water quality variables (temperature, dissolved oxygen saturation, salinity, nitrate + nitrite nitrogen, ammoniacal nitrogen, total nitrogen, dissolved reactive phosphorus, total phosphorus, suspended solids and chlorophyll a), water level and number of hours dry (dewatered) the month before sampling were included in the analysis. P values from RDA output up to < 0.1 were accepted as significant (Lepš & Šmilauer 2003). ANOVA and regression analyses were conducted in PRIMER 5 and ordinations in CANOCO.

3.4 Results

3.4.1 Spatial patterns in water quality

Water chemistry conditions varied spatially, with the eastern most end of the lake (Kaituna Lagoon) having different chemistry from the southernmost end (Taumutu). The three other sites (Greenpark Sands, Selwyn Huts and Timberyard) were more similar to each other (Table 3.2). Temperature and dissolved oxygen concentrations differed little around the lake. Spot temperatures ranged from 4.8 – 29°C with highest temperatures at Kaituna Lagoon and Greenpark Sands. Four of the chemical parameters analysed showed significant spatial variation (salinity, ammonia nitrogen, total nitrogen and chlorophyll a) and seasonal change (nitrate + nitrite nitrogen, total nitrogen, dissolved reactive phosphorus and total phosphorus; Table 3.2). Highest salinity concentrations occurred near the lake opening at Taumutu (mean = 6.9 ppt) and lowest concentrations at the opposite end of the lake (Kaituna Lagoon; mean= 4.0 ppt). Spot salinity measurements at Taumutu and Kaituna were significantly different (Tukey's test, q = 5.674, $P < 0.01$). Ammonia nitrogen (NH_3N) concentration varied significantly around the lake, but no effect of season was found (Table 3.2). Concentrations of NH_3N were significantly higher at Greenpark Sands than Kaituna, Timberyard, Mid Lake and Taumutu (Tukey's test; Table 3.2). Mean nitrite and nitrate nitrogen (NNN) concentrations were similar across all sites, and varied with season (Table 3.2). NNN concentrations were significantly higher in autumn and winter compared to summer (q = 4.409, $P < 0.05$; q = 4.704, $P < 0.01$). High concentrations of NH_3N and NNN were found at Greenpark Sands (NH_3N mean = 0.053 mg/L; NNN mean = 0.05 mg/L). Total nitrogen concentrations were lowest at Selwyn Huts (mean = 0.296 mg/L) and highest at Kaituna Lagoon (mean = 0.625 mg/L). No significant difference in either dissolved reactive phosphorus (DRP) or total phosphorus (TP) concentrations between sites in the lake (Table 3.2). Seasonally, the highest concentrations of both DRP and TP were observed over summer months decreasing through the remainder of the year. Suspended solids showed no significant difference spatially or seasonally in the lake (Table 3.2). Significant difference in chlorophyll *a* concentrations around the lake were found, but no seasonal effect (Table 3.2). Highest chlorophyll *a* concentrations were found at Timberyard and Taumutu, decreasing towards Kaituna Lagoon.

Table 3.2 Water chemistry parameters for 5 sites around Lake Ellesmere/Te Waihora collected monthly from January – December 2009.

		Kaituna n=11	Greenpark n=9	Selwyn n=12	Timberyard n=12	Taumutu n=12	Spatial ANOVA $F_{5,63}$ Stat	*P* value	Seasonal ANOVA $F_{3,64}$ Stat	*P* value
Temp (°C)	Mean	14.4	14.5	12.8	12.9	12.6				
	SE	1.9	2.3	1.7	1.7	1.6				
DOSAT (%)	Mean	91	108	113	113	110				
	SE	8	8	4	5	3				
Salinity (ppt)	Mean	4.9	6.2	6.6	6.7	6.9	**4.214**	**0.003**	0.838	0.478
	SE	0.7	0.8	0.5	0.4	0.4				
NH_3N (mg/L)	Mean	0.021	0.053	0.025	0.019	0.015	**3.263**	**0.011**	0.211	0.888
	SE	0.006	0.016	0.006	0.005	0.004				
NNN (mg/L)	Mean	0.041	0.050	0.052	0.052	0.036	0.741	0.545	**5.029**	**0.003**
	SE	0.021	0.023	0.020	0.024	0.015				
TN (mg/L)	Mean	1.629	2.400	2.233	2.283	2.300	**4.081**	**0.003**	**6.201**	**0.0009**
	SE	0.181	0.187	0.086	0.090	0.111				
DRP (mg/L)	Mean	0.024	0.026	0.029	0.024	0.024	0.165	0.925	**6.039**	**0.001**
	SE	0.007	0.011	0.009	0.009	0.007				
TP (mg/L)	Mean	0.234	0.288	0.250	0.248	0.253	0.79	0.56	**9.645**	**0.0001**
	SE	0.036	0.033	0.017	0.019	0.021				
SS (mg/L)	Mean	151	226	233	230	248	1.74	0.139	1.59	0.127
	SE	32	61	17	22	20				
Chl a (*u* g/L)	Mean	50	96	128	142	128	**5.528**	**0.0005**	0.791	0.648
	SE	10	15	11	11	12				

3.4.2 Water level

Water level data collected from barometric divers followed a similar pattern to that shown by the permanent recorder at Taumutu (Figure 3.3; Appendix 2). Water levels were highest over winter from May to July and lowest during August through to October after the lake had remained open or 6 weeks. Taumutu generally had deeper water levels than the other four sites, with water levels generally showing a rapid response to lake openings (Figure 3.3; Appendix 2). This was not surprising as this recorder is close to the opening. Wind events also drive water levels around the lake (Figure 3.3). These can be localised effects (as observed at Taumutu) when strong south easterly winds caused a ~0.9 m increase over four days in November (Figure 3.3), or generate whole lake level shifts, such as when a strong north east wind blows, causing a decrease water level at one side of the lake and an increase at the other (Figure 3.3).

Once water levels reached the opening winter trigger value of 1.13 m (Taylor 1996) at the end of May 2009, opening procedures were initiated. From June through July the lake opened five times. The first opening on 6^{th} June lasted 7 days and resulted in a 0.4 m drop in water level (Figure 3.3). Opening was again initiated on the 24th June but was unsuccessful, and the lake had closed within 48 hours on the high tide. On the 1st and 8th of July the lake was opened for 4 consecutive days, resulting in a decrease of 0.2 m and 0.04m, respectively (Figure 3.3). The lake was successfully opened for an extended duration that reduced water level from 22nd July to 3rd September (44 days). Lake levels were reduced from 1.27 m to a minimum of 0.31 m, a 0.9 m reduction (Figure 3.3). From closure to the end of the year (31st December 2009) mean lake level was 0.87 m, peaking over a nine day period (discussed above) to 1.85 m and reaching a minimum of 0.56 m in October, both events driven by wind (Figure 3.3).

Water level varied from small changes (< 0.01 m) either increasing or decreasing from minutes to hours (< 2 hours), or larger fluctuations (> 0.01 m) lasting for hours (> 2 hours) to days (Figures 3.3 & 3.4). In the month prior to invertebrate sampling in summer and autumn at Taumutu, the eulittoral zone was continuously covered with water and in the month prior to the winter sampling event, the eulittoral zone was dewatered periodically for approximately 17 days (423 hrs; Table 3.3).

Table 3.3 Amount of time during which the eulittoral zone was either wet or dry at five sites in August 2009 (* periodic).

	Eulittoral Dry water level (m)	Wet day of sampling hours	Dry day before hours	week before hours	month before hours
Kaituna	< 0.1	0	24	168	405*
Greenpark	< 0.18	0	24	168	637*
Selwyn	< 0.08	5*	4*	8*	89*
Timberyard	< 0.15	4*	24	145.5*	508*
Taumutu	< 0.5	22*	0	63*	423*

Based on the water level at Taumutu and its relationship with other site locations, an estimation of daily water level fluctuations was made for each location from January to April 2009 (Figures 3.3 & 3.4). These estimates suggest that the eulittoral zone was continually dry from January to April at all sites and that the eulittoral zone was continually covered with water in the month prior to autumn sampling. However, over the month prior to winter sampling, the eulittoral zone was frequently inundated with water at all locations (Table 3.3; Figure 3.4). At Timberyard, the zone was frequently watered and dewatered during the month and week prior winter sampling (Table 3.3; Figure 3.4A) and the day before and the morning of invertebrate sampling, the eulittoral zone was frequently dewatered and watered (Figure 3.4B). Selwyn Huts, Greenpark Sands and Kaituna Lagoon also experienced intermittent periods of water inundation the month before winter sampling; for 4 days (89 hrs), 26 days (637 hrs) and 17 days (405 hrs), respectively (Table 3.3). Timberyard, Greenpark Sands and Kaituna Lagoon were all dry the day before sampling.

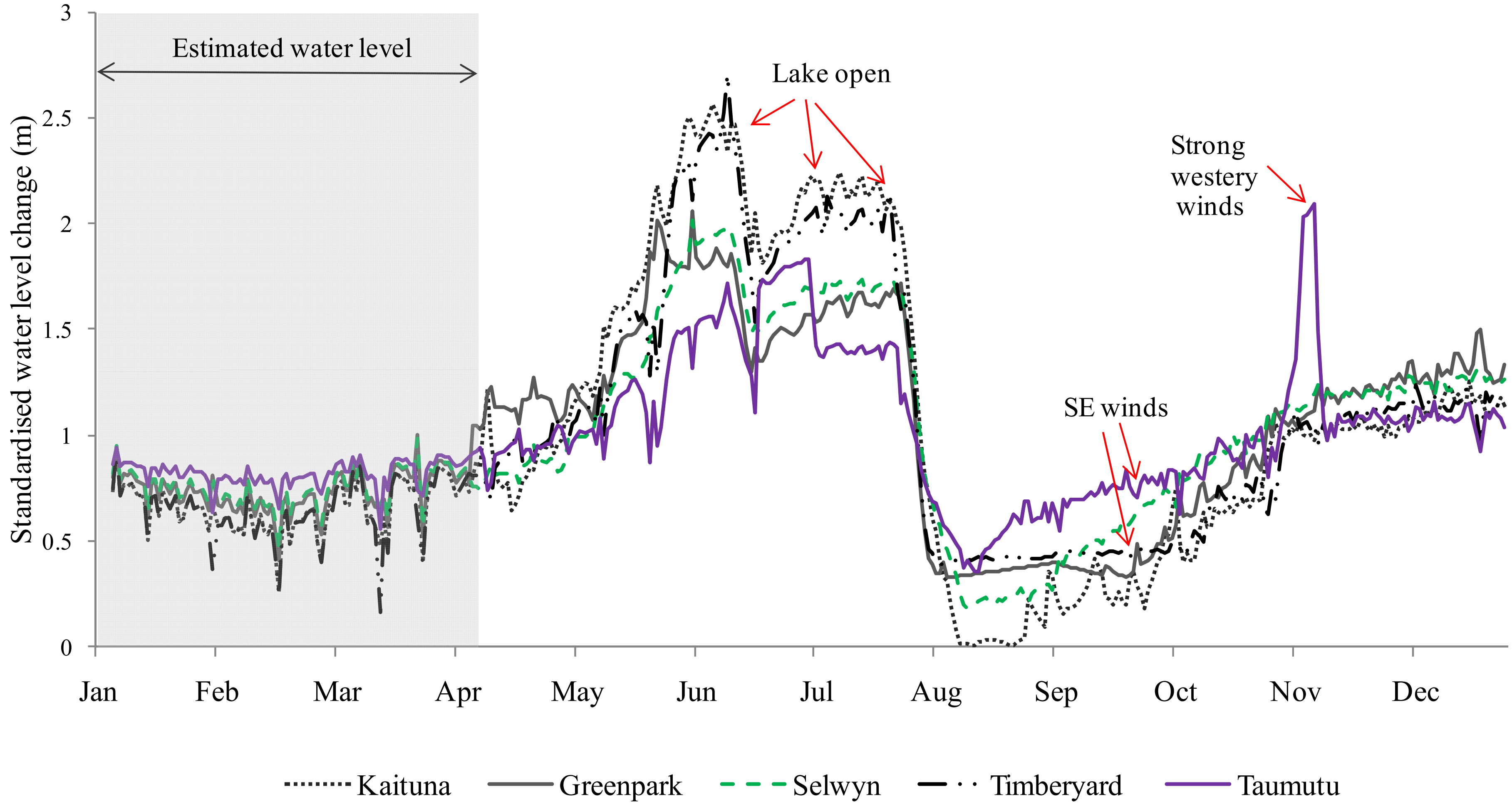
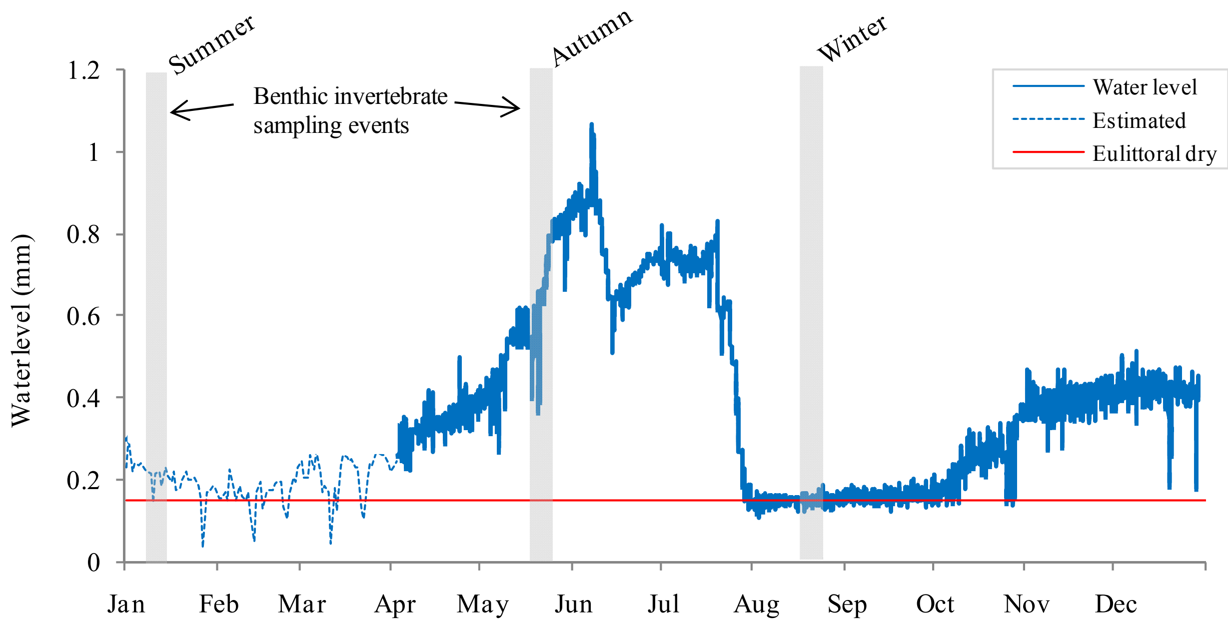


Figure 3.3 Standardised daily mean lake level from January to December 2009 at five locations around Lake Ellesmere/Te Waihora. The gray block indicates the period when water level was estimated.



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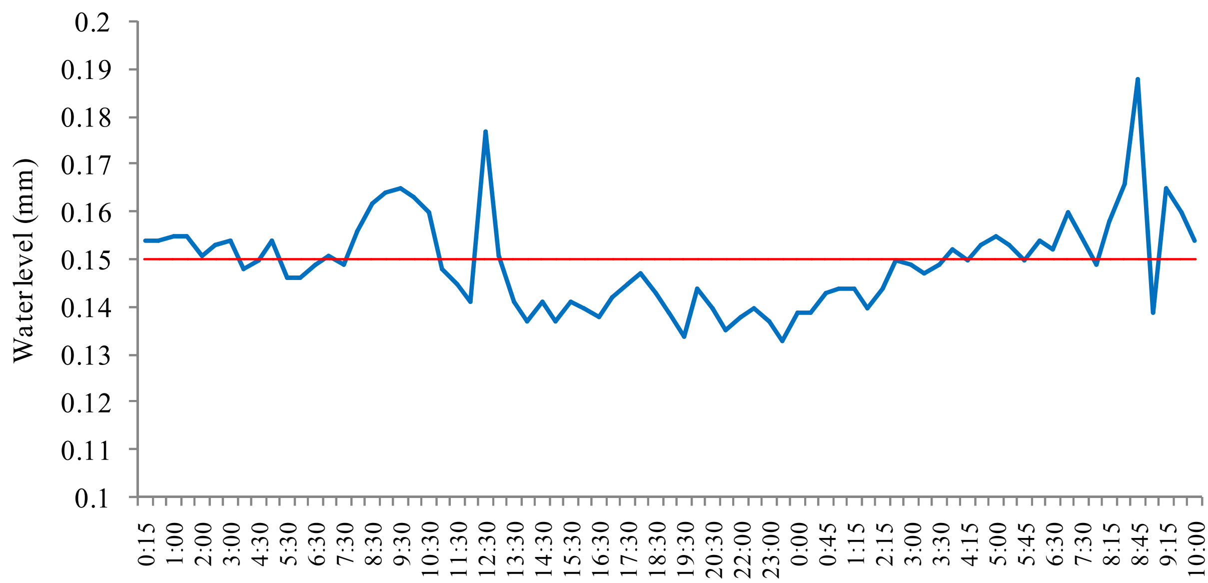


B

Figure 3.4 A) Water levels at Timberyard, January – December 2009. B) Water level at Timberyard the day before and morning of invertebrate sampling on August 26th 2009. Below red line indicates when eulittoral zone has no covering water (< 150 mm).

3.4.3 Do invertebrate communities differ along the longitudinal gradient?

A total of 28 invertebrate taxa were recorded in the eulittoral zone, 15 in the mid-littoral and 18 in the lower littoral zone (Table 3.4). Invertebrate taxonomic richness differed significantly between the eulittoral, mid-littoral and lower littoral zones around the lake (One-way ANOVA, $F_{2,30} = 4.252$, $P = 0.0237$; Appendix 3). Higher numbers of taxa were found at eulittoral sites, and richness was significantly higher than at mid-littoral zones (Tukey's test $q = 4.122$, $P < 0.05$), but not the lower littoral zone. Taxonomic richness differed significantly along the littoral zone in Kaituna Lagoon (One-way ANOVA, $F_{3,4} = 11.87$, $P = 0.021$. Kaituna Lagoon was the only location to have significantly more taxa in the eulittoral (19 taxa) and lower littoral (15 taxa) zones than the mid-littoral zone (8 taxa; Tukey's test, $q = 6.203$, $P < 0.05$, $q = 5.908$, $P < 0.05$). The lowest number of taxa was observed in the littoral zone at Taumutu, where 13 species were recorded in the eulittoral zone, and 6 taxa recorded in the mid-littoral zone.

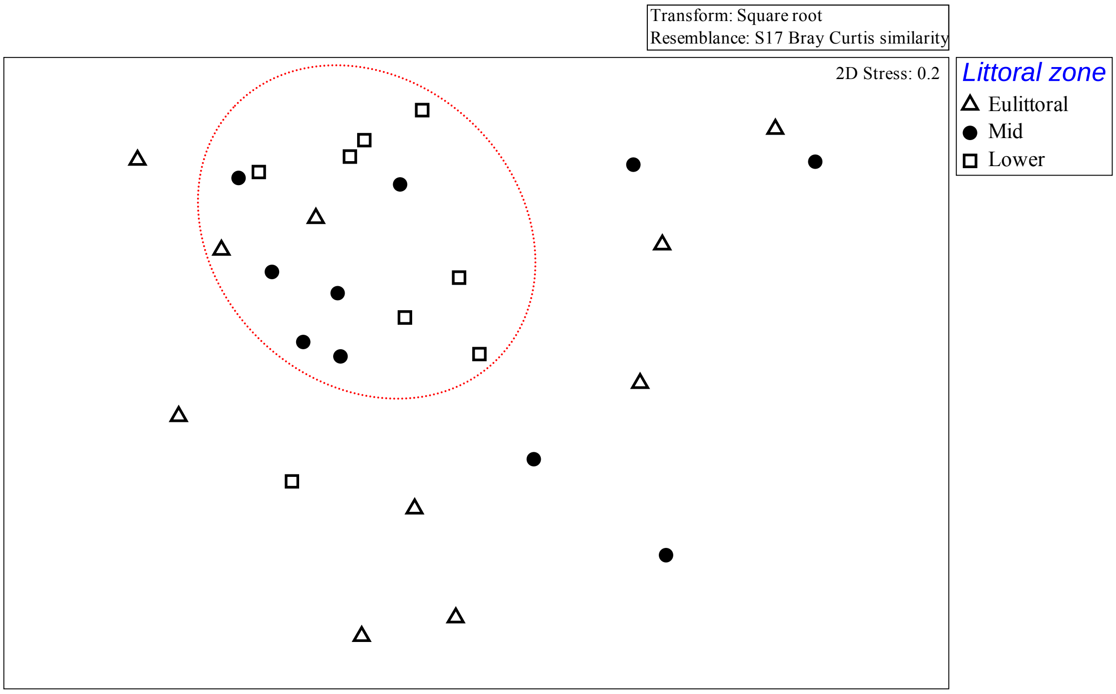
Mean density of invertebrates was highest in the eulittoral with 8600 ind. m^{-2}, lowest in the mid-littoral (6700 ind. m^{-2}), slightly increasing in the lower littoral zone (7500 ind. m^{-2}). Multi-dimensional scaling showed the benthic invertebrate composition differed along the littoral zone gradient, although not significantly (ANOSIM: R-statistic = 0.03, $P = 0.22$; Figure 3.5A; Appendix 4). Although not significant (ANOSIM, Pairwise test; R-statistic = 0.149, $P = 0.054$; Appendix 4) invertebrate composition in the eulittoral zone was most different from that in the lower littoral zone. Mid-littoral and lower littoral zone sites were more similar in invertebrate composition (Figure 3.5). Mollusca, *Potamopyrgus antipodarum* and oligochaeta dominated the benthic community in the eulittoral zone, comprising 38% and 30% of the community, respectively (Figure 3.5B). One-way ANOVA (with autumn excluded) showed mollusc density significantly declined further out in the lake ($F_{2,24} = 3.912$, $P = 0.034$). Crustaceans (43%) and oligochaetes (26%) dominated the mid-littoral littoral zone. The midge *Chironomus zealandicus* was also abundant, comprising 17% of mid-littoral zone invertebrates. In the lower littoral zone crustaceans were the dominant taxa (52%) followed by oligochaetes (22%) and molluscs (18%). Trichoptera, Coleoptera, Nematoda, Platyhelminthes and polychaete taxa were grouped in the 'Other' category (Figure 3.5B). The trichopterans *Oecetis unicolor*, *Oxyethira albiceps* and *Paroxyethira*, Coleoptera; (Hydraenidae) and the dipterans *Austrosimulium,* Ephydridae, Stratiomyidae and Tipulidae including *Zelandotipula* were mainly found in eulittoral samples (Table 3.4). Nematodes and polychaetes were found across the littoral zone gradient but were in higher densities in the eulittoral zone than mid-littoral and lower. Platyhelminths were found in higher densities in the lower littoral zone than in the eulittoral and mid-littoral zones.

Table 3.4 Benthic invertebrate taxa in the eulittoral (n=15), mid-littoral (n=10) and lower (n=8) littoral zone in Lake Ellesmere/Te Waihora over three seasons 2009 (+ denotes presence of taxa) and mean density of seven dominant taxa in the lake (ind.m^{-2}).

Taxa		**Eulittoral**	**Mid**	**Lower**
Trichoptera	*Oecetis unicolor*	+		+
	Oxyethira albiceps	+		+
	Paroxyethira sp.	+		
Coleoptera	Hydraenidae	+		
Diptera	*Austrosimulium* sp.	+		
	Ceratopogonidae	+	+	+
	Empididae	+	+	+
	Ephydridae	+		
	Stratiomyidae	+		
	Tipulidae	+		
	Zelandotipula sp.	+		
Chironomidae	*Chironomus zealandicus*	+	+	+
	Orthocladiinae	+		+
	Tanypodinae	+	+	+
Mollusca	*Potamopyrgus antipodarum*	+	+	+
	Potamopyrgus estuarinus	+		
	Physa	+		
Crustacea	*Austridotea annectens*	+	+	+
	Copepoda	+	+	+
	Isopoda	+		
	Ostracoda	+	+	+
	Paracorophium excavatum	+	+	+
	Tenagomysis chiltoni	+	+	+
Nematode	Nematoda	+	+	+
Oligochaeta	Oligochaeta	+	+	+
Platyhelminthes	Platyhelminthes	+	+	+
Polychaeta	*Scolecolepides benhami*	+	+	+
	Dipolydora sp.	+	+	+
Total number of taxa		28	15	18

Taxa	**Eulittoral***		**Mid**		**Lower**	
Av density (ind.m-2)	Mean	SE (n=10)	Mean	SE (n=10)	Mean	SE (n=8)
Potamopyrgus antipodarum	2603	1016	558	123	755	362
Paracorophium excavatum	2689	1350	3742	1327	4798	1540
Oligochaeta	1845	812	1405	384	1002	185
Chironomus zealandicus	882	370	700	295	382	146
Austridotea annectens	177	115	28	21	404	359
Ostracoda	82	76	22	14	6	4
Polychaeta	46	28	50	25	46	17
Tenagomysis chiltoni	50	25	78	30	58	40

* Autumn data excluded



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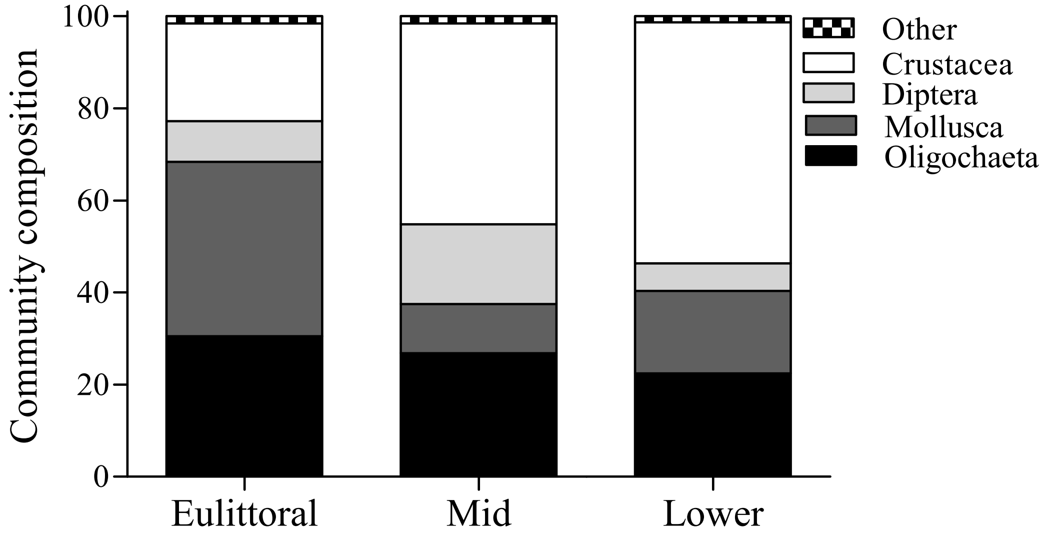

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Figure 3.5 Invertebrate data collected in the Eulittoral (n=10), Mid-littoral (n=10) and Lower-littoral (n=8) over summer & winter 2009 in Lake Ellesmere/Te Waihora (May samples not included). A) MDS invertebrate composition along the littoral zone. Red-dotted elliptical indicates grouping of similar sites. B) Invertebrate composition. 'Other' includes; Trichoptera, Coleoptera, Nematoda, Platyhelminthes and Polychaeta.

3.4.4 Are there spatial differences around the lake in richness and community composition?

Taxonomic richness was spatially similar around the lake (One-way ANOVA, $F_{4, 28} = 1.24$, $P = 0.316$). Kaituna Lagoon had the greatest taxonomic richness in the littoral zone with 20 species recorded. Similar taxonomic richness was observed at Greenpark Sands (16), Selwyn Huts (15) and Timberyard (17). The lowest number of taxa was observed in the littoral zone in Taumutu (13) taxa.

Invertebrate density in the littoral zone significantly differed with location (One-way ANOVA, $F_{4,28} = 4.618$, $P = 0.005$; Figure 3.6A). The highest number of invertebrates was recorded in the littoral zone at Selwyn Huts (mean, 11000 ind. m^{-2}; Figure 3.6A). Tukey's multiple comparison test showed Selwyn Huts had significantly higher individuals per m^2 than Kaituna Lagoon ($q = 4.418$, $P < 0.05$) and Taumutu ($q = 5.317$, $P < 0.01$).

Multidimensional scaling (MDS) ordination of the invertebrate community across all sampled locations revealed marked differences in community composition that differed significantly between sites (ANOSIM; R-statistic = 0.192, $P = 0.002$; Figure 3.6B; Appendix 4). Invertebrate composition in the littoral zone of Kaituna and Taumutu were most different to each other, and Greenpark Sands, Selwyn Huts and Timberyard were similar to each other (Figure 3.6B). Invertebrate composition in both Kaituna Lagoon and Taumutu were significantly different to that at Greenpark Sands, Selwyn Huts and Taumutu (Figure 3.6B; Appendix 3). *C. zealandicus* were less abundant at Selwyn Huts, while *P.excavatum* increased compared to Greenpark Sands and Timberyard (Figure 3.7). Kaituna Lagoon had the most diverse community composition, but lower densities than other locations, and included *Oecetis unicolor*, Ceratopogonidae, and Tipulidae. Chironomidae were almost absent from Taumutu and the dominance of crustacea was reduced compared to other sites (Figure 3.7). Four taxa groups dominated composition in the littoral zone of Lake Ellesmere/Te Waihora, the crustacea (*P. excavatum*) comprising around 30% of recorded taxa, oligochaetes (26%), molluscs (25%) and *C. zealandicus* (12%; Figure 3.7). In addition to the four dominant taxa, four others of the 28 recorded, were found at all locations around the lake: *Austridotea annectens*, *Tenagomysis chiltoni,* Platyhelminthes and polychaeta. Trichoptera and diptera species were primarily recorded at Kaituna Lagoon and were largely absent from Taumutu.

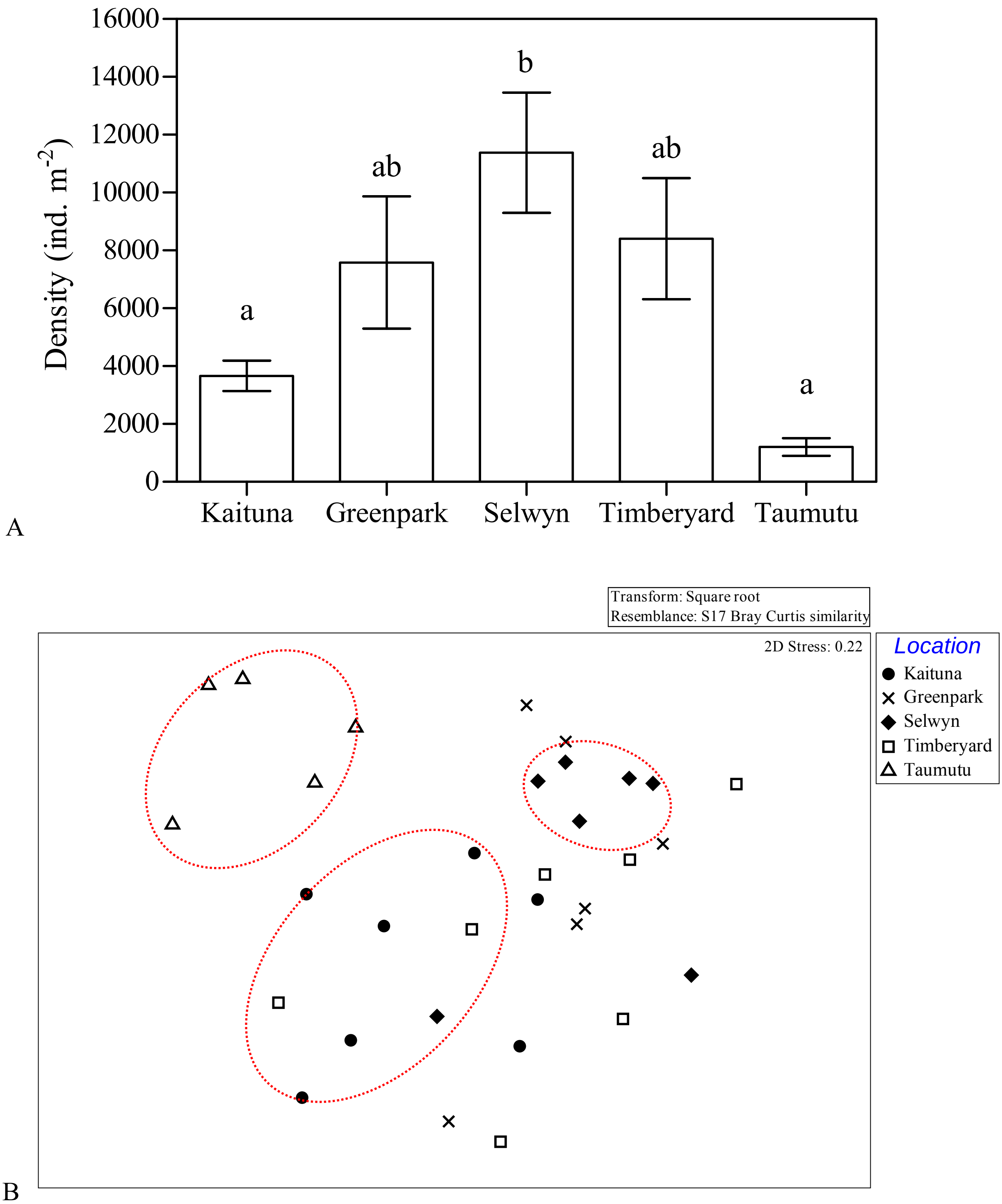


Figure 3.6 A) Density of benthic invertebrates in the littoral zone of Lake Ellesmere/Te Waihora based on samples collected on three occasions in 2009 (Mean ± 1SE). Different letters above bars indicates significant differences. B) MDS ordination of invertebrate communities at 5 locations around the lake. Red-dotted ellipticals indicate grouping of similar sites.

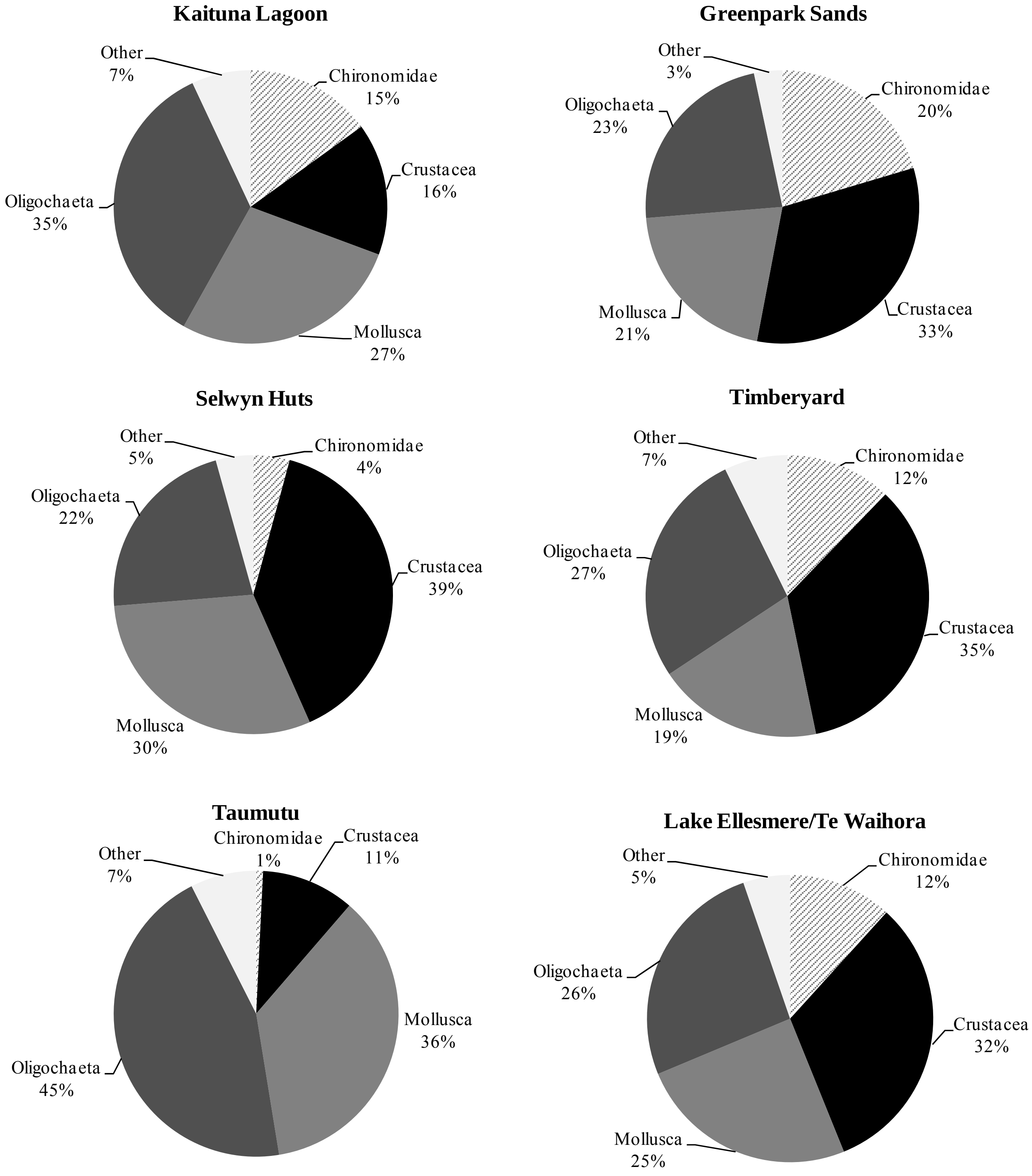


Figure 3.7 Invertebrate composition in the littoral zone of Lake Ellesmere/Te Waihora based on samples collected in 3 seasons in 2009.

3.4.5 Do benthic invertebrate communities change seasonally?

Total taxonomic richness in the littoral zone was higher in summer (24) than winter (18). Within the littoral zone, the eulittoral zone had higher taxonomic richness in autumn (25) than summer (17), and winter (16). Richness varied less with season in the mid-littoral (12 in summer and 14 in winter) and lower littoral zones (11 in summer and 13 in winter), but was generally higher in winter than summer.

Mean invertebrate density in the littoral zone was highest in summer with 1500 ind. m^{-2}, decreasing to 950 ind. m^{-2}, in winter. One-way ANOVA showed a significant effect of season on density in the eulittoral zone ($F_{2,320} = 7.833$, $P = 0.0005$). Tukey's multiple comparison test showed significantly more individuals per m^2 in summer than autumn ($q = 5.596$, $P < 0.001$; Figure 3.9A), but no significant difference to winter ($q = 2.257$, $P > 0.05$).

Benthic invertebrate community composition varied from season to season in the littoral zone. MDS ordination showed community composition significantly differed from summer to winter (ANOSIM; F-statistic = 0.117, $P = 0.02$; Figure 3.8B; Appendix 4). Over summer, *P. antipodarum* and *P. excavatum* dominated the littoral zone (Figure 3.9). In contrast, over winter crustaceans were still dominant, but *P. antipodarum* became less abundant, while *C. zealandicus* became more abundant (Figure 3.9). Composition in the eulittoral zone changed significantly with season (ANOSIM; F-Statistic = 0.312, $P = 0.079$; Figure 3.9; Appendix 4). *P. antipodarum* was dominant in the eulittoral zone throughout the year, with density decreasing by 50% from summer to winter (Figure 3.9). In contrast, densities of Oligochaeta and *C. zealandicus* increased from summer to winter (Figure 3.9). Crustacean taxa decreased in autumn, particularly *P. excavatum,* which was almost absent (2%). The benthic composition in the mid-littoral and lower littoral zone was similar across seasons. *P. excavatum* dominated 62% of the benthic composition and was only slightly more abundant in summer than winter. Two taxa, *Paroxyethira* and Orthocladiinae were only found over summer. Six taxa were only collected in autumn but in low numbers, four being diptera taxa; *Austrosimulium,* Ephydridae, Stratiomyidae and *Zelandotipula*, as well as *Physa acuta* and Isopoda. Only one taxon, Tipulidae (excluding *Zelandotipula*) was found in winter but not summer or autumn.

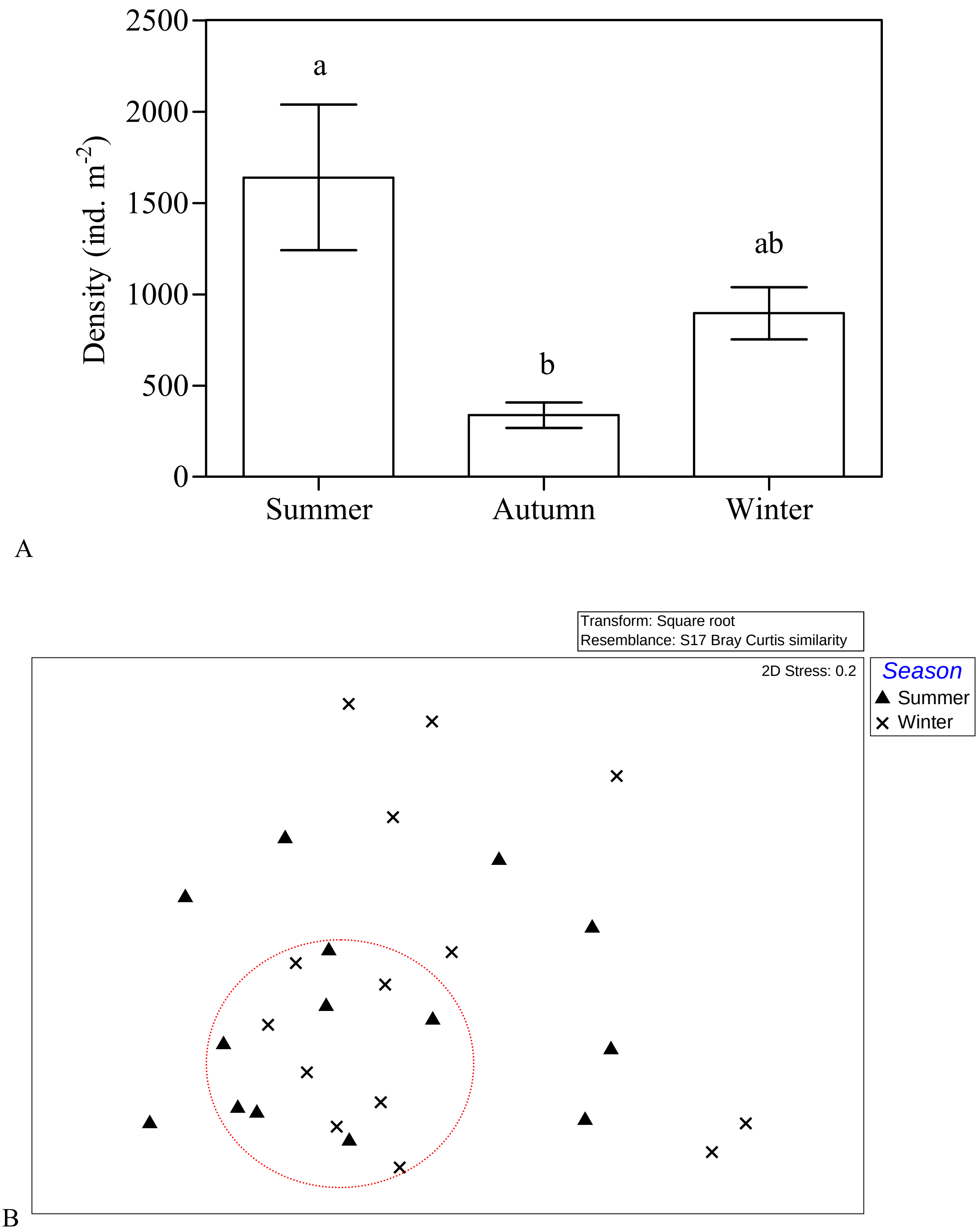


Figure 3.8 A) Benthic invertebrate density in the eulittoral zone of Lake Ellesmere/Te Waihora (Mean ± 1SE) over summer and winter 2009. Different letters above bars indicates significant differences. B) MDS ordination showing seasonal change in invertebrate community composition. Red-dotted elliptical indicates grouping of similar sites.

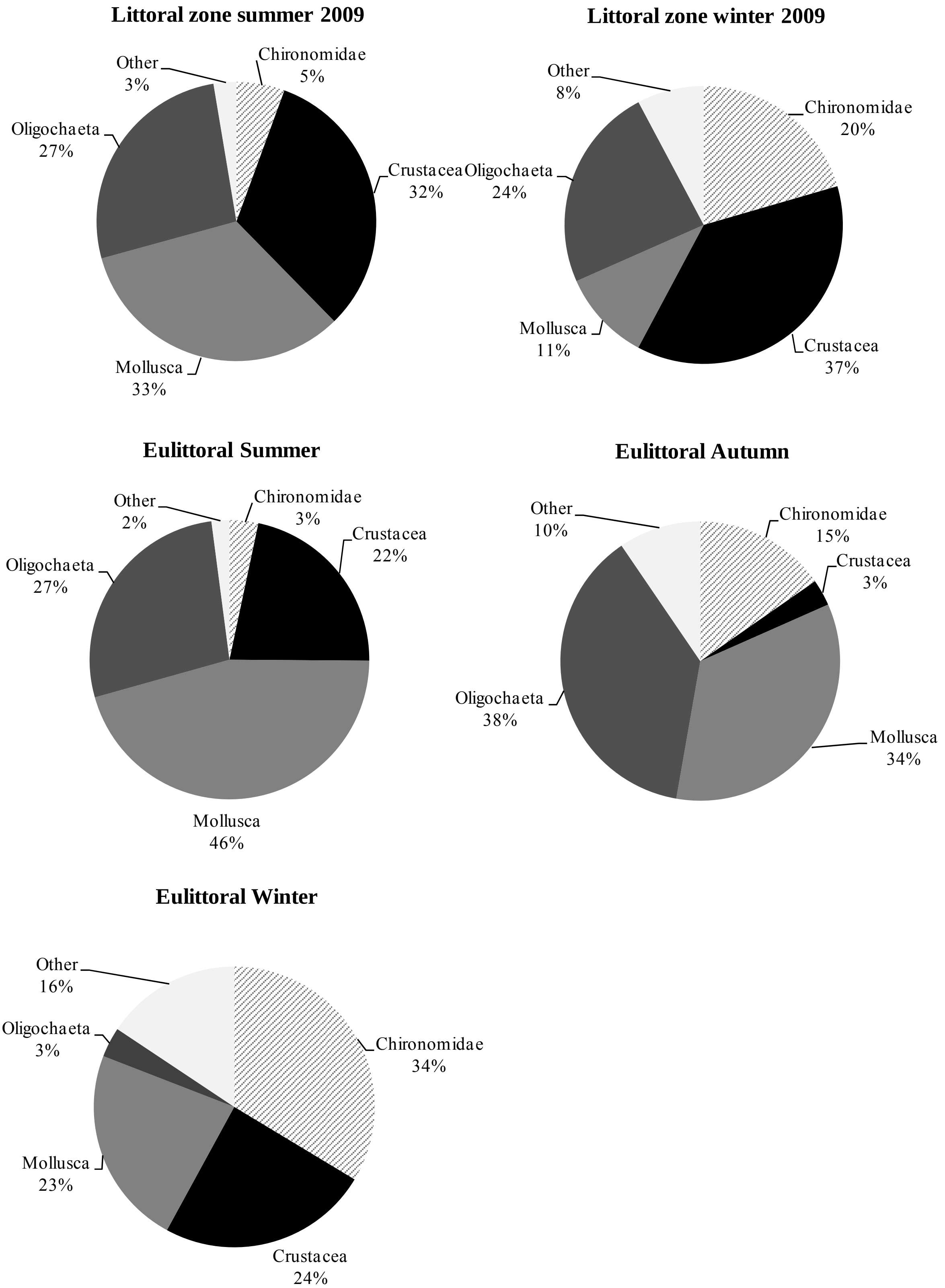


Figure 3.9 Seasonal invertebrate composition in the littoral zone of Lake Ellesmere/Te Waihora over 2009.

3.4.6 How are invertebrate communities distributed in relation to environmental variables in the littoral zone?

Linear regression analysis showed total taxonomic richness changed in relation to position along the littoral gradient. Taxonomic richness in the eulittoral zone was significantly related to water level (r^2 = 0.561, P = 0.001; Figure 3.10A), increasing as water level increased. A significant negative relationship was observed in the mid-littoral zone (r^2 = 0.498, P = 0.023), with taxonomic richness decreasing with increasing water levels. No correlation was found in the lower littoral zone (Figure 3.10A). Average invertebrate density was generally higher at lower water levels. Although, average density was not significantly related to position along the littoral zone, in either the eulittoral (r^2 = 0.19, P = 0.102), mid-littoral (r^2 = 0.13, P = 0.297) or lower (r^2 = 0.13, P = 0.389; Figure 3.10B). Total invertebrate density (Figure 3.10C) and taxonomic richness (Figure 3.10D) were normally distributed in relation to ambient salinity. At both high and low levels of salinity, density and richness of invertebrates were low, but at mid-range salinities, invertebrate density and richness were high. The curves fitted in Figure 3.10B and C are Gaussian fits with respective r^2 values of 0.174 and 0.120.

Redundancy analysis (RDA) of invertebrate communities and environmental variables indicated that the most important factors driving site differentiation along the littoral zone gradient were temperature (F = 2.919, P = 0.028), water level (F = 3.371, P = 0.034) total phosphorus (F = 2.909, P = 0.034) chlorophyll *a* (F = 2034, P = 0.07) and hours dry in the previous month (F = 1.799, P = 0.1; Figure 3.11). Other variables such as salinity, suspended solids and dissolved oxygen were important but not significant. Temperature, which is directly related to season, chlorophyll *a* and total phosphorus, appear to drive composition in the mid-littoral and lower littoral zone of the lake over winter. These sites were characterised by taxa such as polychaetes and crustaceans. At higher temperatures, the eulittoral zone often experiences more frequent periods of dewatering. The amount of time dry in the eulittoral zone in the month prior to sampling was found to drive invertebrate distribution and composition, with such species as *C. zealandicus* commonly occurring. Water level tended to drive invertebrate composition in the eulittoral zone around the lake; the mid-littoral and lower littoral zone where water was generally deeper, had different dominant invertebrates to the lower water eulittoral zones (Figure 3.11). At lower water levels the eulittoral zone was characterised by molluscs and worms. Conversely, when water levels were high in the eulittoral zone, more mobile taxa such as copepods and isopods were more abundant and consequently community diversity increased.

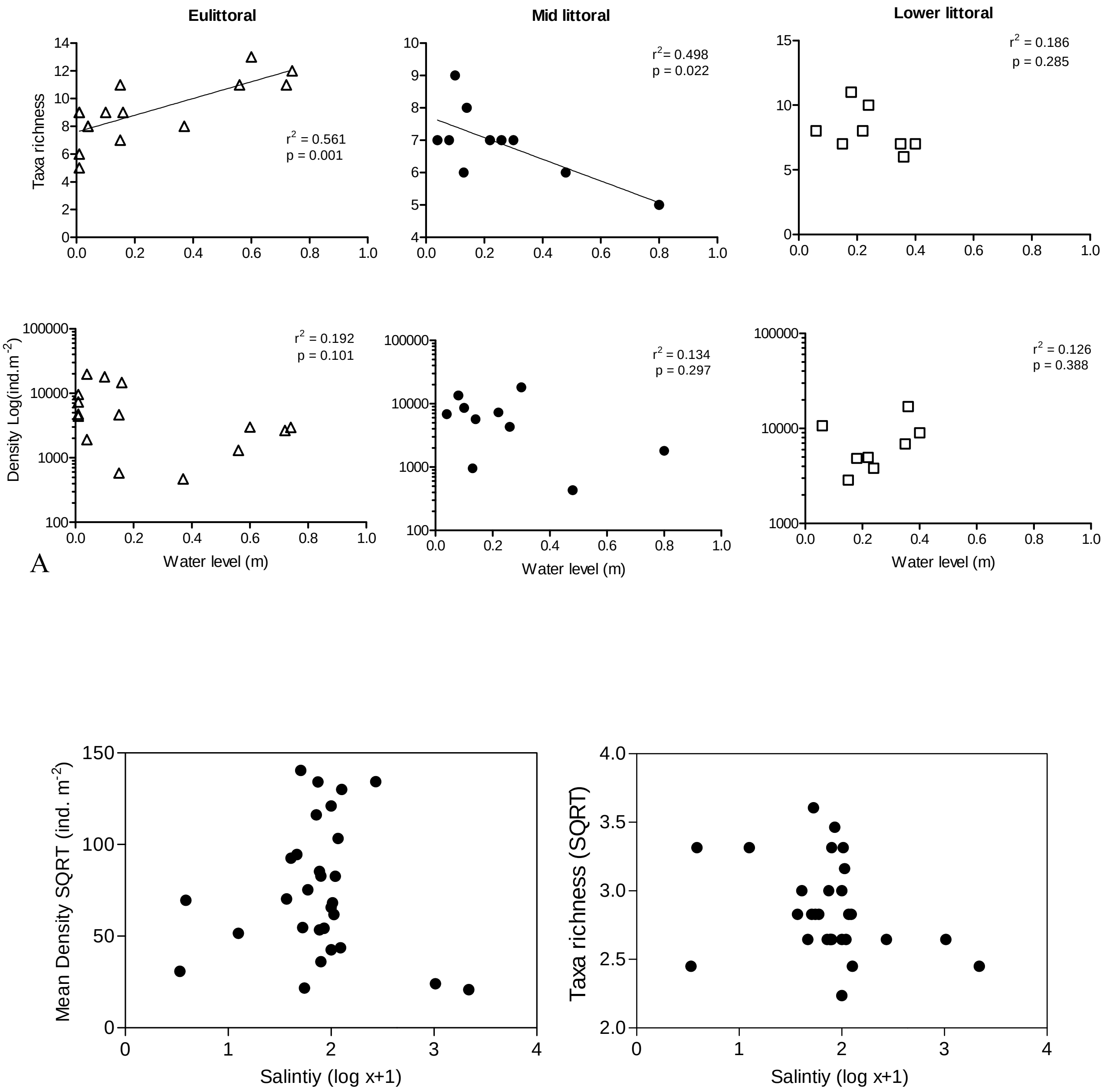


Figure 3.10 A) Linear regressions of taxon richness and density log(ind.m^{-2}) on water level in the eulittoral (open triangle), mid-littoral (solid circle) and lower littoral (open square) zones, B) the relationships of invertebrate density and C) taxa richness with salinity at 5 sites sampled in 3 seasons in 2009.

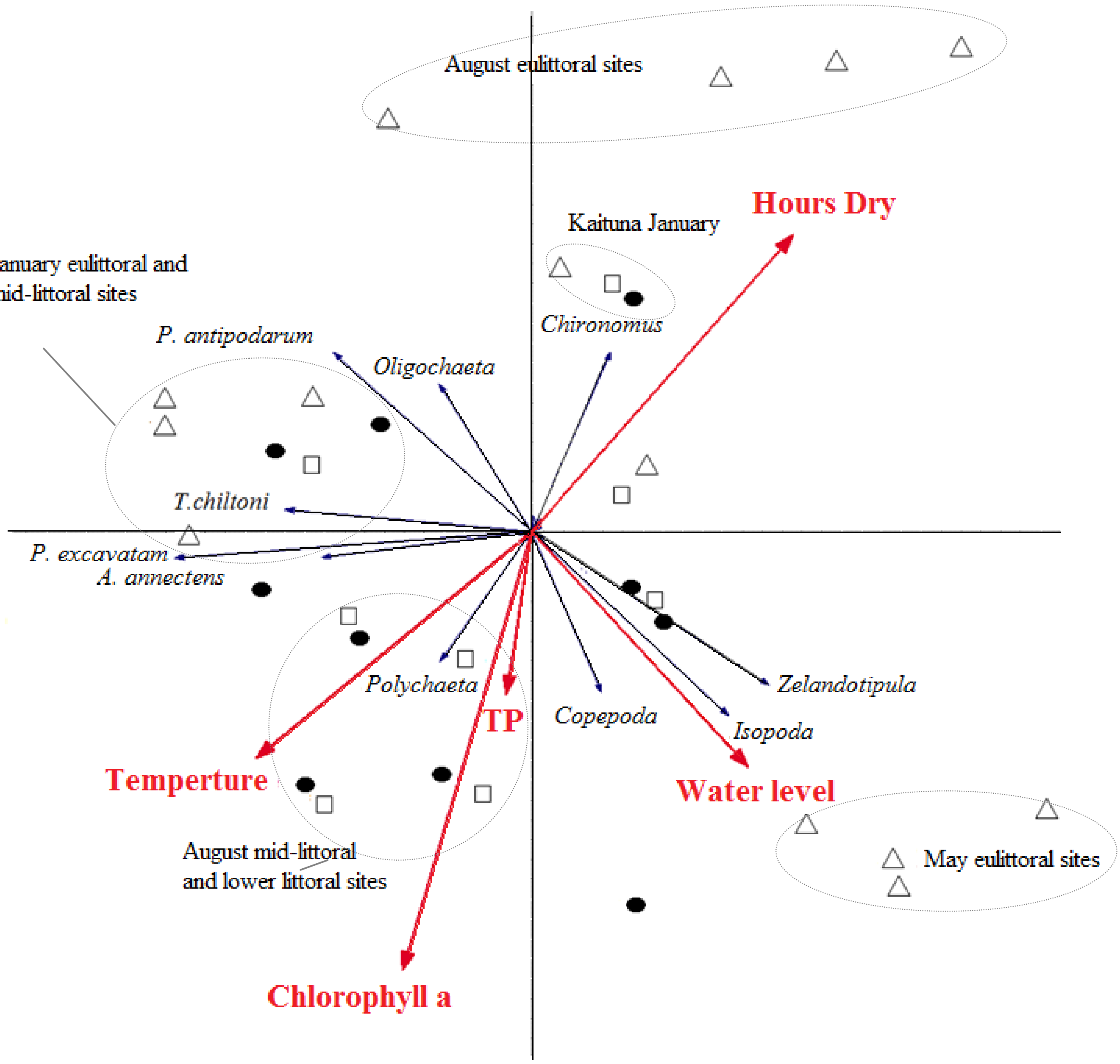


Figure 3.11 RDA of benthic invertebrates sampled in three seasons in 2009 and significant environmental variables (temperature, water level, total phosphorus (TP), hours dry in the previous month and chlorophyll a) in the littoral zone of Lake Ellesmere/Te Waihora (open triangle = eulittoral site, solid circle = mid-littoral and open square = lower littoral zone sites).

3.5 Discussion

3.5.1 Invertebrate taxonomic richness and composition

Invertebrate richness and density varied significantly around Lake Ellesmere/Te Waihora, both within and between sites. In particular, the gradient along the littoral zone had a large effect on both taxonomic composition and density of the invertebrate communities, a pattern previously unidentified in the lake. Differences in invertebrate composition and density around the lake were found to be related to water quality variables, such as temperature, total phosphorus and habitat conditions such as water level change. Furthermore, taxonomic richness of the lake was high in comparison to other coastal lakes in New Zealand (Schallenberg & Waite 2003; Thompson & Ryder 2003), although this is likely due to differences in sampling method. Taxonomic richness was relatively similar to some inland lakes (Mylechreest 1978; Biggs & Malthus 1982), but low compared with high country, freshwater lakes in New Zealand (James *et al*., 1998). The number of invertebrate taxa found in this study was 28 species, which is higher than previous studies in this lake, with only eleven invertebrate species recorded by Kelly & Jellyman (2007) and only eight invertebrate species recorded by Wood (2008). Although 28 species were recorded, benthic invertebrate composition was dominated by four taxa (95 %; *P. excavatum*, oligochaeta, *C. zealandicus* and *P. antipodarum*). Another four taxa frequently occurred throughout the lake but in low numbers (*A. annectens,* Ostracoda, polychaeta and *T. chiltoni*), two of which the isopod and mysid shrimp are highly mobile and not strictly or solely benthic. The other 20 taxa groups were rare spatially and temporally. Kelly & Jellyman (2007) and Wood (2008) used grab sampler and didn't sample in the eulittoral zone which may account for the large difference in taxa number. This suggests sampling methodologies, both design and equipment is important when investigating benthic invertebrate communities. Previous estimates may therefore be severely underestimating the taxonomic richness in the lake, with large HESS samplers, as used in this study, potentially providing the most reliable results.

Invertebrate diversity and density were greatest in the eulittoral zone, with composition becoming more homogenous further out into the lake. Previous research by Yeates (1965) found very high densities of *P. antipodarum*, however recent studies reported molluscs to be largely absent from the benthic fauna in the lake. By sampling along the littoral zone gradient in this study, I found molluscs to be a dominant component of benthic community in the eulittoral zone (30%), with significantly lower abundance in the mid-littoral and lower littoral zones. Anecdotal evidence suggests that large densities of molluscs wash up during severe water level fluctuations and thus are likely to be susceptible to water level fluctuations. Oligochaetes and *C. zealandicus* were found to be the stable taxa of benthic communities in the lake, occurring throughout the lake with generally even distributions across the littoral zone. The crustacean, *P. excavatum*, was the dominant component of the benthic invertebrate community across the littoral zone, increasing in density from the eulittoral (31%) zone, to double the density in the lower littoral zone (64%) where water levels were more stable. As with *P. excavatum,* the density of *A. annectens* doubled from the eulittoral (2%) to the lower littoral zone (5%). Differences in taxonomic dominance are likely related to habitat variables. For example, lower water levels may drive mollusca distribution, and lower water temperatures (driven by higher water levels) may drive *P. excavatum* and *A. annectens* distribution. Benthic invertebrate communities are likely buffered from temperature changes at higher water levels and perhaps those species dominating deeper waters, such as crustaceans, are less able to tolerate high temperatures and periods of desiccation when dewatering occurs.

The eulittoral zone of Lake Ellesmere/Te Waihora has relatively high taxon diversity (28) compared to the rest of the lake (mid-littoral = 15, lower littoral = 18 taxa) and may, therefore, be vital to the lake food-web and supply a large amount of the secondary production to higher trophic levels. The littoral zone represents a relatively large area of Lake Ellesmere/Te Waihora, and these data suggest that invertebrate numbers within this zone may be vitally important to the functioning of the lake. However, this zone is potentially the most threatened by various types of human disturbance such as agricultural development (Hayward & Ward 2009) and water level manipulation (including increased water abstraction, reduced tributary inflow and lake opening events) (Wantzen *et al.,* 2008). Invertebrate densities were relatively high in Lake Ellesmere/Te Waihora compared to other freshwater systems (Timms 1982; James *et al*., 1998; Schallenberg & Waite 2003). This suggests that, primary productivity within the lake supports high numbers of aquatic invertebrates, particularly *C. zealandicus*. Highest densities over summer were consistent with findings of Dawn (1995) and Wood (2008). The high variability in a range of physical variables in the lake has the potential to minimize the distribution of a range of susceptible taxa, but species able to tolerate these conditions appear to be doing extremely well, and had large and healthy populations. Changes in community composition or invertebrate density could have negative flow-on consequences to lake food-webs, and could dramatically affect food supply to higher trophic levels. For example, the decline in juvenile shortfin eel (*Anguilla australis*) growth rates and low abundances of several year classes has been attributed to a shift in dominant benthic invertebrate taxa from molluscs, *P. antipodarum* (Ryan 1986) to the midge *C. zealandicus* over the last 40 years as a result of loss of macrophyte beds (Jellyman *et al*., 1998; Sagar *et al* 2004; Kelly & Jellyman 2007).

3.5.2 Drivers of invertebrate communities

Lake Ellesmere/Te Waihora is exposed to significant shifts in water level over seasonal and daily scales. The shift in water level has the potential to impact invertebrate assemblages over periods of hours to days, whereas seasonal differences in freshwater and saltwater inputs have the potential to affect lake flora and fauna over longer time scales. This is shown by seasonal shifts in species compositions within sites. Temperature variation between seasons has a large effect on species diversity and abundance. The combination of water level fluctuations and high temperature during summer may be having a large impact on desiccation and mortality of many invertebrates. The dominant drivers of invertebrate communities appear to be water level change (driving salinity changes), temperature, nutrient input and habitat availability (Figure 3.11).

The combination of falling water level and high temperature has significant effects on community composition. This was apparent both down a physical gradient of stress (littoral zone gradient) and over time, with changes in water level having a significant influence on community structure (Figure 3.5 & 3.8). Fluctuating water levels associated with wind may play an important role in the wetting of large areas of land, and in certain areas may extend the littoral zone. This has the potential to enhance productivity of the lake, and may extend the habitat of invertebrates, such as *P. antipodarum* and *C. zealandicus*, which are able to withstand periods of emersion (*see* Chapter 4). However, the water level drop associated with opening of the lake, which can last for longer periods (> 1 week), could cause areas of lake bed to become dry, and the associated invertebrate community may suffer high mortality (presumably this already happens and has occured for many decades). Furthermore, assemblages associated with fully submerged habitats are less likely to be resistant to desiccation than assemblages that are frequently exposed to fluctuating water levels.

Unlike inland water bodies, Lake Ellesmere/Te Waihora is subject to large fluctuations in salinity due to marine inputs. This has the potential to be a major driver of the invertebrate community, as some aquatic species cannot tolerate fluctuating saline concentrations (James *et al.,* 2003; Kefford *et al.,* 2003). Therefore, major variations in salinity, either high or low, have the potential to negatively affect survival of lake flora and fauna. Furthermore, non-lethal effects of salinity change have the potential to affect reproductive output and therefore, recruitment of juveniles (James *et al.,* 2003). Evidence from this research indicates large differences in salinity (average and maximum) between the sampling sites in Lake Ellesmere/Te Waihora. This variation in salinity was associated with large differences in the density of invertebrates found at each site. At both high and low salinity, invertebrate density was relatively low, but at mid-levels of salinity (2-7 ppt) invertebrate density was variable (Figure 3.11B). This suggests that the invertebrates living in the lake are likely to be adapted to the lower mid-range of salinities common in coastal lakes (Drake *et al*., 2009), and fluctuations above or below this range may affect the relative biomass of invertebrates within the lake. Furthermore, the duration of salinity increase, particularly at the higher end of the scale is likely to significantly impact invertebrate survival. As in many brackish water systems, taxa diversity is limited to species that are able to tolerate relatively large variations in salinity (Remane 1934). Although at any one time, salinity may be within the range of a number of species, the seasonal variation in salinity may have large effects on invertebrates adapted to a narrow range of salinity.

In my opinion lake levels should be managed to maintain optimum invertebrate diversity and density to maximise lake productivity and health. The eulittoral zone of Lake Ellesmere/Te Waihora provides suitable foraging habitat for thousands of avian species which visit annually (O'Donnell 1989), and the abundant benthic invertebrate community supports these large numbers (Hughey & O'Donnel 2009). Furthermore, the lake has abundant populations of several fish species such as shortfin eel, common bully, smelt and flounder, all supported by the benthic invertebrate community (Jellyman & Smith 2009). Although extreme (> 1 m) water level changes are necessary at times to ensure neighbouring communities do not get flooded, extended periods of low lake levels can have detrimental effects on avian breeding ecology and success (Miers & Williams 1969), water quality and benthic invertebrates. Conditions which provide the highest quality and widest range in micro-habitats for benthic invertebrates are provided by intermediate lake levels associated with a slowly rising or falling lake level.

3.5.3 Implications for lake management

Currently, major lowering of lake water levels are regulated by human intervention to stop flooding onto fringing farmland. Opening of the lake to the sea has an immediate and large influence on lake salinity near the lake outlet. Salinity concentrations at sites not near the outlet increase gradually after the opening of the lake, with the extent of change largely depending on how long the lake is open (Figure 2.12) and strength of wind driving mixing. Increasing levels of salinity have the potential to negatively impact invertebrate density and composition. However, lake openings generally occur in the winter during high levels of freshwater input, thereby decreasing the risk of elevated salinities, and potentially levelling out lake-wide salinity to somewhere close to the optimum range. The extent and duration of drawdown, coupled with the time of year, are important drivers of benthic invertebrate composition in Lake Ellesmere/Te Waihora (Figure 3.8 & 3.9). The current water level opening regime and trigger levels, primarily result in the lake being opened during winter months and would likely have less detrimental impacts on benthic fauna than openings over summer due to less risk of dessication. The dominant benthic community seems to be well adapted to the dynamic nature of the littoral zone as it is present year round and particularly species inhabiting bottom sediments. If lake levels were maintained at slightly higher levels than at present over summer (~0.6 m), it would likely have significant benefits for benthic invertebrate populations, by reducing desiccation risk and extreme temperatures (*see* Chapter 4), while increasing habitat availability (including birds and fish). Furthermore, an increase in invertebrate abundance should have positive flow on effects through the food web, including improved growth and reproduction of bird populations and fish.

The present study has identified potential drivers affecting the ecology of Lake Ellesmere/Te Waihora. In particular, falling lake levels during the summer months could severely affect invertebrate fauna in the littoral zone, with potentially large flow-on consequences for the fisheries of the lake. Decreasing river input due to intensification of farming could restrict freshwater inputs, and coupled with increased evaporation, further reduced lake levels could have long lasting effects on invertebrate abundance. Based on calculations of when the eulittoral zone was dry at Kaituna Lagoon, Greenpark Sands, Selwyn Huts and Timberyard and the water level at Taumutu (msl), I was able to establish a minimum lake level to which the eulittoral zone would be protected from excessive water level reduction. I suggest a minimum lake level at Taumutu of 0.6 m over summer months December – March in order to protect benthic invertebrate communities in the eulittoral zone from extensive loss of habitat, extreme temperature and reduced risk of desiccation.

Chapter 4

Exploring mechanisms for the effects of lake level fluctuations on benthic invertebrate communities

4.1 Abstract

In order to examine factors affecting the survival of benthic invertebrates in Lake Ellesmere/Te Waihora and factors likely to inhibit predatory invertebrates, which are currently absent from the lake, I experimentally tested the role desiccation, predation pressure and salinity tolerance had on key invertebrate taxa. Desiccation experiments on benthic invertebrates from the lake showed short durations of dewatering, irrespective of temperature, reduced survival of more mobile taxa with thin exoskeletons, such as crustaceans. *Tenagomysis chiltoni* significantly decreased (40% survived) after 6 hrs dry, and *Paracorophium excavatum* significantly decreased (40% survived) after 12 hrs dry at 25 °C. The sediment dwelling midge, *Chironomus zealandicus* and the isopod *Austridotea annectens* were tolerant, with 100% survival after 24 hrs dry at 25 °C. Predatory invertebrates, dragonfly larvae, *Procordulia grayi,* damselfly larvae, *Xanthocnemis zealandica,* backswimmer, *Anisops wakefieldi* and waterboatmen, *Sigara arguta* differed in their response to fish predation and salinity concentration. Predation pressure, mediated by the absence of macrophyte refugia and turbidity affected the damselflies and waterboatmen, respectively. Salinity may be affecting the recruitment of some predatory invertebrates (e.g., *Anisops wakefieldi*), but is clearly not the primary causal factor for the absence of all predatory invertebrate species. Benthic invertebrates in the littoral zone of the lake appear to be adapted to periods of intermittent dewatering, and even sustained dewatering under cooler temperatures. However, extended water level drawdown, would have significant impacts on the survival of a number of lake taxa. Thus, whilst the benthic fauna of Lake Ellesmere/Te Waihora appear to be adapted to frequent episodes of water level change, their response is dependent on temperature and total time spent dry. Multiple factors and interactions from predation pressure, salinity and lack of macrophytes are likely responsible for the absence of predatory invertebrates in Lake Ellesmere/Te Waihora. The current lake opening regime is favourable to benthic invertebrate survival as the lake is predominantly open over winter when temperatures are lower, reducing the risk of desiccation. Reducing nutrient loading through improved riparian vegetation, fencing of tributaries and lake margins and improved farm management are needed if aquatic diversity is to be improved.

4.2 Introduction

Benthic invertebrates constitute a significant biomass and play an important role in overall production in lake ecosystems (James *et al.* 1998; Free *et al*. 2009). Littoral zones of shallow lake ecosystems can be highly dynamic and characterised by variable physical conditions and strong wind and wave action (Verschuren *et al.* 2000; Aroviita & Hämäläinen 2008). It is the interface between the terrestrial environment and open water, receiving, processing and modifying inputs from the surrounding catchment (Scheffer 2001; Kelly & McDowall 2004; Free *et al*., 2009) and is frequently a region of high biodiversity and productivity. In Lake Ellesmere/Te Waihora, the littoral zone covers a considerable area of the lake and processes affecting this zone probably have a strong influence on the ecology and productivity of the whole lake. In Lake Ellesmere/Te Waihora the littoral zone is continually expanding and contracting due to fluctuating water levels driven by wind and wave forces and manual opening events.

Studies of whole lake biodiversity and function have provided insights into the environmental factors that govern invertebrate community composition (Hanson 1990; Weatherhead & James 2001; Tolonen *et al.* 2001; Strayer *et al*., 2003; Kelly & Hawes 2005). Small-scale local factors, such as habitat complexity have been demonstrated to have greater influence on benthic communities than large-scale factors such as the geographical position of the lake (Johnson & Goedkoop 2002). In the littoral zone, differences in substrate composition (e.g., cobbles, sand, silt, macrophytes or woody debris) have been shown to be the most important factors in determining community composition and abundance (James *et al.,* 1998; Verschuren *et al.,* 2000; Tolonen *et al.,* 2001; Weatherhead & James 2001; Free *et al.* 2009; Takamura *et al.* 2009). Other factors have also been shown to be important including; wind exposure (Allan & Kirk 2000), cyanobacterial blooms (Oberholster *et al.* 2009), dissolved oxygen and nutrient levels (Petridis 1993; Free 2009), water depth and fluctuation (Kato *et al.* 1990; Frazer *et al.* 1998; Thompson & Ryder 2008; McEwen & Butler 2010) and salinity (Williams 1999; Verschuren *et al.* 2000). However, a gap in our understanding remains as to the relative importance of environmental factors in determining invertebrate community composition in the littoral zone of shallow brackish lakes. In particular, the interaction between water level fluctuations and salinity on littoral invertebrates in brackish lakes, have not been well studied.

4.2.1 Water level fluctuations

Changing water levels and increased water level fluctuation can be amongst the most important anthropogenic disturbances to lake ecosystems (Richter *et al.* 1997, Coops *et al.* 2003). Most of the existing knowledge on the effects of water level fluctuations on lake systems has been derived from studies on reservoirs or regulated lakes, where water level fluctuations of up to 20 m can occur (Smith *et al.* 1987). These fluctuations have been shown to directly affect the littoral zone through desiccation and/or freezing of exposed substrates (Coops *et al.,* 2003). Benthic invertebrate communities can be particularly affected by water level change due to the low mobility of some taxa restricting their ability to follow receding water (Slepukhina 1996). Thus, extensive dewatering of the littoral zone has been shown to negatively affect benthic invertebrate richness and abundance, particularly in the eulittoral zone (Currier 1954; Palomaki 1994; Blinn *et al.* 1995; Prus *et al.* 1999; Richardson *et al.* 2002). Some lakes undergo natural, seasonal, changes in water levels although the amplitude of fluctuations is often small. Furthermore, within lakes experiencing natural fluctuations, the highest invertebrate diversity and biomass may be found in the eulittoral zones (Czachorowski 1993). Thus, it is changing the natural regime of water levels, rather than water level change *per se*, which causes an alteration of eulittoral habitats, with associated impacts on eulittoral invertebrates. The magnitude of the impacts of fluctuating water levels upon invertebrate communities depend upon the tolerances of individual species to desiccation, their colonisation strategies, and the duration and timing of fluctuations, whether short term (e.g. hours), or long term (e.g. days or weeks; Johnson & Goedkoop 2002). For example, the snail *Potamopyrgus antipodarum* can withstand harsh environmental conditions such as high temperatures (28°C; Winterbourn 1969) and long periods of desiccation when in moist substrate (Upto 15 days; Badie & Rondelaud 1982; Mostafa 2009). However, Mostafa (2009) found survival rates of the mollusc, *Biomphalaria arabica* to rapidly decrease when exposed to desiccation in the absence of moist soils after 36 hours.

4.2.2 Salinity

Many plants and animals have become adapted to a wide range of aquatic environments and have developed a range of physiological mechanisms to maintain the necessary balance of water and dissolved ions in cells and tissues (osmoregulation). Salinity primarily affects the occurrence of species through its link with osmoregulatory physiology (Hart *et al.* 1991;

Withers 1992). Several studies have recorded a decrease in lake invertebrate taxonomic richness as salinity concentrations increase (Williams & Williams 1998; Kefford *et al.* 2003; Piscart *et al.* 2006; Jeppesen *et al.* 2007; Ellis & Macisaac 2009). Tolerance to salinity can also change during different stages of an organism's life cycle (Hart *et al*., 1991). However, other factors may confound these effects. For example, high temperatures have been shown to reduce the ability of aquatic invertebrates to cope with increasing salinity. Furthermore, the presence of a species within a given salinity range does not necessarily indicate that its population is self-sustaining, as certain life stages may be more resistant to variation in salinity than others (Kefford *et al.* 2004). The traditional view is that as salinity rises (from a baseline level) there is no effect, until some threshold is reached, after which sub-lethal effects, such as reduced growth and reproduction occur (Hart *et al.* 1991). If salinity increases further, death will result, eventually. However, studies on freshwater gastropods (Kefford *et al*., 2003), fish (Boeuf & Payan 2001) and a cladoceran (Yang & He 1997), have shown that rather than having a threshold response, individuals often do best at an intermediate salinity and worst at high or low salinities. There is thus an inverted 'U' shaped salinity concentration response curve (Clark *et al.,* 2004). At very low ambient salinities, animals are hyper-osmotic (internal osmolarity higher than medium) and active transport of salt ions is necessary to maintain internal osmolarity, at a large energetic cost. Conversely, at high ambient salinity, animals are hypo-osmotic (internal osmolarity lower than the medium), and will lose water to the surrounding water causing dehydration unless water loss can be minimized (Davenport 1985).

4.2.3 New Zealand lake fauna

Invertebrate species richness in New Zealand lakes is relatively low compared to many lakes elsewhere (Winterbourn & Lewis 1975; Mylechreest 1978; Forsyth 1987; Sanders 1996; Kelly & MacDowall 2004). Several studies have noted that invertebrate predators are relatively common in our alpine lakes (Crumpton 1977; Biggs & Malthus, 1982; Talbot & Ward 1987; Crumpton 1997). Predatory invertebrates occupy an intermediate position in the foodweb, where they are both predators of other invertebrates and the prey of fish (Johnson 1991). Biggs & Malthus (1982) found the damselfly larvae (*Xanthocnemis zealandica*), dragonfly larvae (*Procordulia grayi*) and predatory caddisfly larvae (*Hydrobiosis parumbripennis*) to be abundant in the littoral vegetation zone of several lakes in the upper

Clutha Valley. However, Schallenberg & Waite (2004) noted that invertebrate predators have not been widely reported in our coastal lakes, and when present were found in low numbers. Prior to 1964 before the Lake Ellesmere/Te Waihora underwent a regime shift, the water was clear and macrophyte beds were abundant throughout the lake. At this time a species of waterboatmen, *Sigara arguta* and damselfly larvae were present in the lake (Hughes *et al.* 1974). However, three separate studies conducted in Lake Ellesmere/Te Waihora, found that the invertebrate fauna was depauperate, comprising only 8 taxa, and that invertebrate predators were absent (Yeates 1965; Kelly & Jellyman 2007; Wood 2008). In summer 2009 at Kaituna Lagoon, at the south-east end of Lake Ellesmere/Te Waihora, a semi-permanent pond separated from the lake by a 1 m buffer strip of vegetation (which during high lake levels overflowed into the pond), I observed abundant populations of three of the four predatory invertebrate species used in my experiments; *X. zealandicus*, backswimmers and waterboatmen (none have been found in the main lakes itself). Several factors may be responsible for the current absence of invertebrate predators in the lake. One possible explanation is an inability to withstand desiccation or frequent disturbance caused by water level fluctuations. Other possible explanations include predation pressure, the loss of macrophytes (which historically provided habitat and refuge from fish and bird predation), greater variation in salinity concentrations (due to changes in lake hydrology), or a combination of these factors.

The aims of this chapter were firstly to investigate the ability of key invertebrate taxa to survive periods of desiccation. This was done experimentally by manipulating wetting and drying conditions for several representative invertebrate taxa. Additionally, I experimentally explored three possible mechanisms that might inhibit predatory invertebrates in Lake Ellesmere/Te Waihora. Specifically, I tested the response of several typical lake invertebrate predators to fish predation pressure, lack of macrophytes and tolerance to saline concentrations. I predicted that the benthic fauna of Lake Ellesmere/Te Waihora would be adapted to frequent periods of desiccation, but that temperature and length of desiccation period would be important to their survival. Secondly, I hypothesised that a combination of predation pressure, lack of macrophytes and fluctuating saline concentrations would have varying impacts on different predatory invertebrates.

4.3 Methods

4.3.1 Site description

Lake Ellesmere/Te Waihora is a shallow (< 2 m deep) brackish lake, covering an area of 20,000 ha. It has an extensive littoral zone. The eulittoral zone is subjected to varying degrees of water level fluctuation. Water level changes can be small (< 0.10 m) but frequent and driven by wind and wave action, or large (> 1 m) and lasting for days to weeks, when the lake is artificially opened.

4.3.2 Invertebrate tolerance to desiccation

In order to determine the impact of variations in water level on littoral zone invertebrates I selected four species commonly found in the lake; midge: *Chironomus zealandicus,* isopod*: Austridotea annectens,* crustaceans: *Paracorophium excavatum* and *Tenagomysis chiltoni* and tested their resistance to desiccation. Ten replicate individuals of each species were placed separately in a plastic dish (on 10 ml of damp lake bed sand/mud on 500 μm mesh) and subjected to three different scenarios at 11°C ± 0.1 and 25 °C ± 0.2, with survival recorded. Mesh was pulled tight to suspended invertebrates out of water, then lowered down into the water according to the experiment (Figure 4.1). Smaller individuals (< 200 μm long) such as *P. excavatum* were placed on 5 ml of substrate in a petri dish, wetted and dried with a syringe (Figure 4.1).

- **Experiment one**
  - Intermittent fluctuation: Dry for 1 hr, wet for 5 mins, dry for 2 hrs, wet for 5 mins, dry for 3 hrs, wet for 5 mins, dry for 4 hrs, wet for 5 mins, dry for 5 hrs, wet for 5 mins, wet for 6, hrs
- **Experiment two**
  - Short term drawdown: 6 hrs dry, 10 minutes wet, 6 hrs dry.
- **Experiment three**
  - Long term drawdown: 24 hrs dry
  - Immersion: 24 hr wet

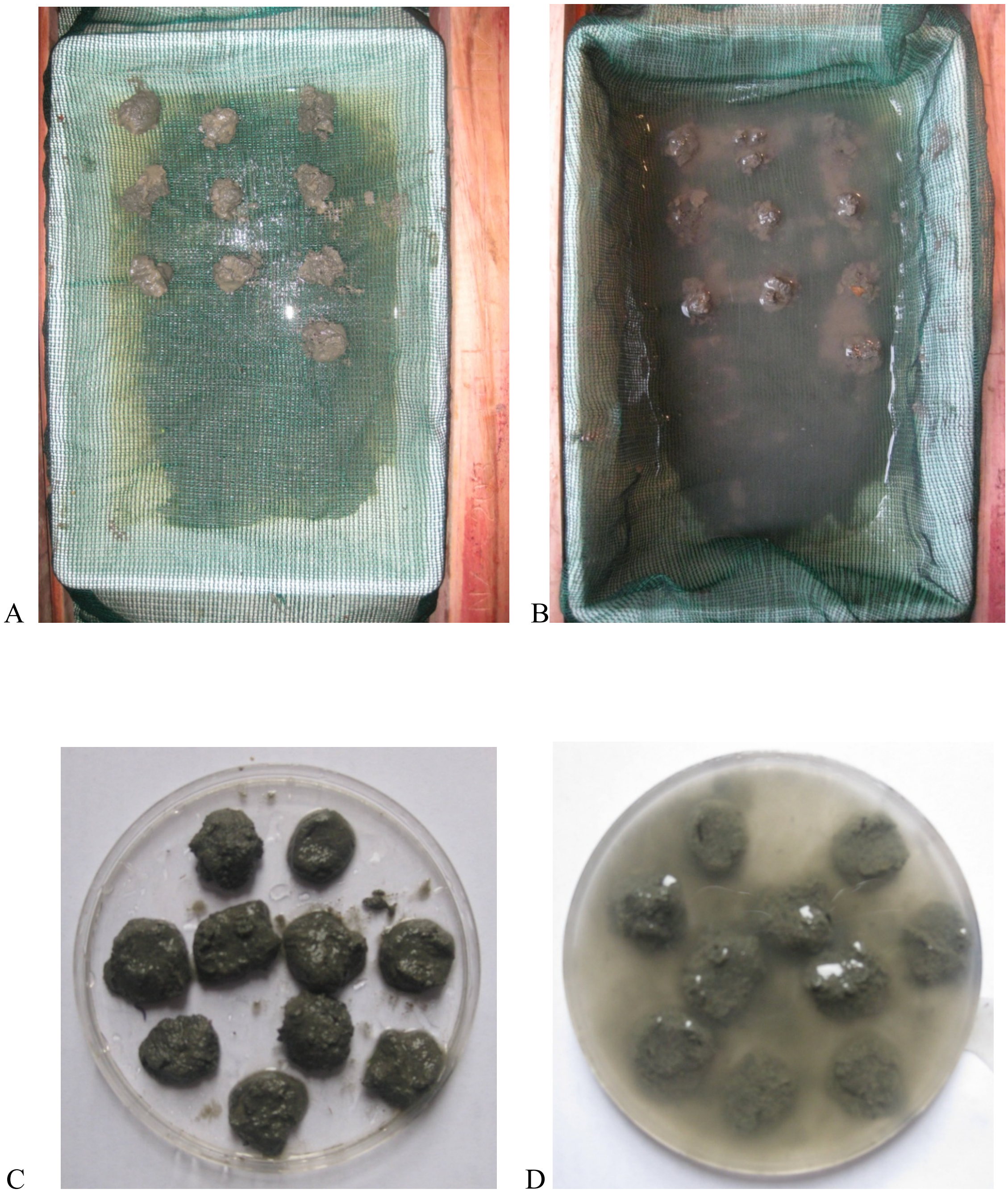


Figure 4.1 Desiccation experiment; A) Invertebrates on material mesh and lake bed sand/mud substrate, tightened and out of water: B) Mesh lowered, invertebrates underwater: C) Petri dish with smaller invertebrates when dry: D) Petri dish when wet.

4.3.3 Response to predation pressure

Predatory invertebrates appear to be absent from Lake Ellesmere/Te Waihora, therefore I tested the survival ability of several common invertebrate predators in the presence of the most abundant fish predator in the lake, the common bully, *Gobiomorphus cotidianus*. *G. cotidianus* are very abundant in the littoral zone of the lake, thus one possible explanation for the absence of predatory invertebrates might be predation pressure from fish. Predation might be mitigated by macrophytes (which historically were abundant in the lake) and turbidity. Four predatory invertebrate species were tested. Larvae of the damselfly *Xanthocnemis zealandica,* the backswimmer, *Anisops wakefieldi* and the waterboatmen, *Sigara arguta* were collected with a hand held net (250 μm mesh) from a pond near McLeans Island, Christchurch. Dragonfly nymphs, *Procordulia grayi* were collected from Lake Sarah, in the high country of Canterbury. Common bullies, *G. cotidianus* were collected from Timberyard Point, in Lake Ellesmere/Te Waihora with a 500 μm seine net. *S. arguta* is not an obligate predator like the other three invertebrates, but feeds largely on submerged plants. However, water boatmen do prey on other insects and can constitute an important intermediate part of lake foodwebs (Savage 1982; Oscarson 1987).

A total of forty plastic tanks (70 L) were set up in a sheltered outdoor area at the University of Canterbury glasshouse complex, ten tanks for each of four treatments; clear water and no macrophytes, clear water with macrophytes, turbid water and no macrophytes, and turbid water with macrophytes. Due to limited availability of dragonfly larvae, each of the four treatments with this predator was reduced to five replicates. Treatments were randomly assigned to reduce the possibility of external environmental conditions affecting results (Figure 4.2). Approximately 2 L of sand was added to the bottom of each tank. Of the 40 tanks, 20 were filled with 30 L of turbid lake water and 20 with 30 L clear water collected from the Selwyn River. Additionally, artificial macrophytes (20 cm x 20 cm) were placed in ten turbid and ten clear water treatments, allowing a comparison of the impact macrophytes may have on the survival of prey. Artificial macrophytes covered half of the tank substrate and were ~ 15 cm under the water surface.

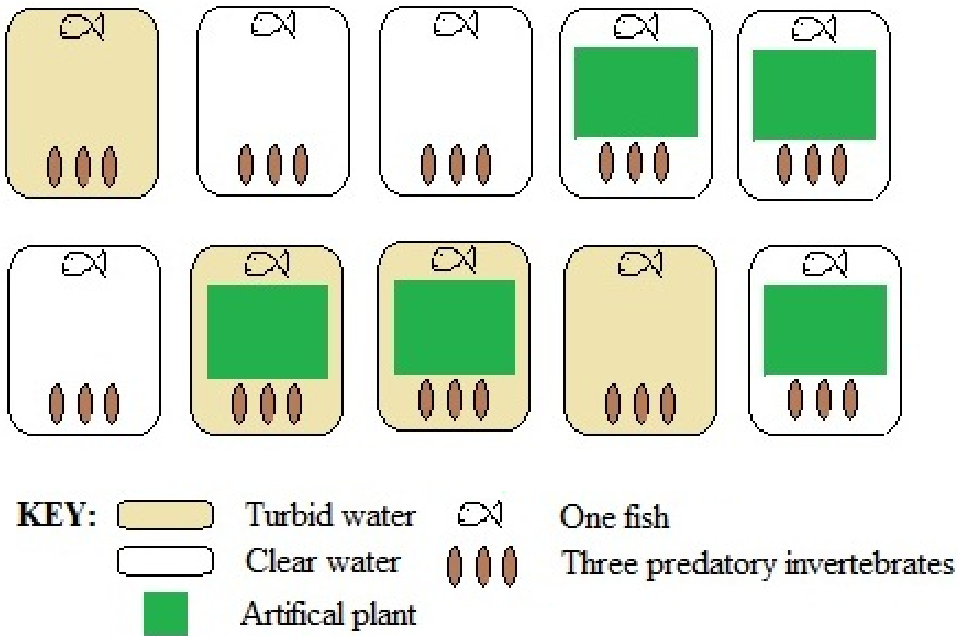


Figure 4.2 Subset of a factorial predator prey randomised experimental block design; ten replicates of each of the four treatments were used.

Predatory invertebrates and fish where collected on the same day where possible. Three invertebrates were added to each tank and left to acclimatise for approximately 6 hrs before a single fish was added. Mesh covers were placed over the mesocosms to prevent prey from escaping, prevent bird predation and limit temperature changes. Each of the four experiments ran for 7 days, with turbid treatments stirred by hand for 10 seconds on days 3 and 5 to maintain turbidity. On the first and last day, spot temperature, dissolved oxygen concentration and salinity were measured in two randomly selected tanks of each treatment. At the end of the experiment fish were removed before remaining water and substrate were filtered through a 500 μm mesh and surviving invertebrates counted. Macrophytes were thoroughly washed and visually inspected to dislodge any prey taxa.

4.3.4 Invertebrate tolerance to salinity

The inability of invertebrates to cope with fluctuating salinity concentrations may be an important limiting factor for invertebrates in the lake as saline intrusion is common. The same four species of predatory invertebrate used in the predation pressure experiment, and two common littoral zone invertebrate species collected from the Lake Ellesmere/Te Waihora, *C. zealandicus* and *T. chiltoni*, were subjected to water of eight different ionic concentrations. Concentrations were 0.1, 2, 5, 6.4, 7.5, 10, 15 and 32.5 ppt salinity, which represents a gradient from fresh to almost full seawater. Freshwater was collected from the Selwyn River, brackish water from Lake Ellesmere/Te Waihora and marine water from Sumner, Christchurch. Concentrations of fresh and saline water were mixed and monitored with a (YSI 30) salinity meter until the desired concentration was achieved. I established ten replicates with 350 ml of each concentration and a single experimental animal. Experiments ran for 96 hrs (4 days) in a temperature controlled room (15 °C). Survival was recorded each 8 am and 6pm for the duration of the experiment.

4.3.5 Statistical Analysis

One and two-way analyses of variance (ANOVA) with Bonferroni post-hoc tests, were used to test for differences in experiments and linear regressions were used to examine relationships between survival and salinity. Values were considered significant when $P <$ 0.05. Analysis was performed in Graph Pad Prism (V5).

4.4 Results

4.4.1 Invertebrate response to desiccation

Water level drawdown/time spent dry, at two different temperatures (25 °C and 11 °C) significantly reduced survival of two of the four benthic invertebrates; *Tenagomysis chiltoni* and *Paracorophium excavatum* (Figure 4.3). *Chironomus zealandicus* and *Austridotea annectens* were relatively tolerant of desiccation in all three experiments, while almost all invertebrates survived in control treatments.

Experiment one

- Intermittent fluctuation: Dry for 1 hr, wet for 5 mins, dry for 2 hrs, wet for 5 mins, dry for 3 hrs, wet for 5 mins, dry for 4 hrs, wet for 5 mins, dry for 5 hrs, wet for 5 mins, wet for 6, hrs.

Three of the four invertebrate taxa, *C. zealandicus*, *A. annectens,* and *P. excavatum* survived all dry periods, irrespective of temperature and length of the dry period (21 hrs in total; Figure 4.3). However, survival of *T. chiltoni* was significantly decreased with exposure time and temperature (Figure 4.3). Two-way ANOVA showed a significant interaction ($F_{6,123}$ = 3.1, $P < 0.0073$) between both time ($F_{1,123}$ = 60, $P < 0.0001$) and temperature ($F_{6,123}$ = 12.3, $P < 0.0001$) on *T. chiltoni* survival. There was a significant effect of temperature after 6 hrs (Bonferroni post-hoc tests , t = 4.229, $P < 0.001$; Figure 4.3).

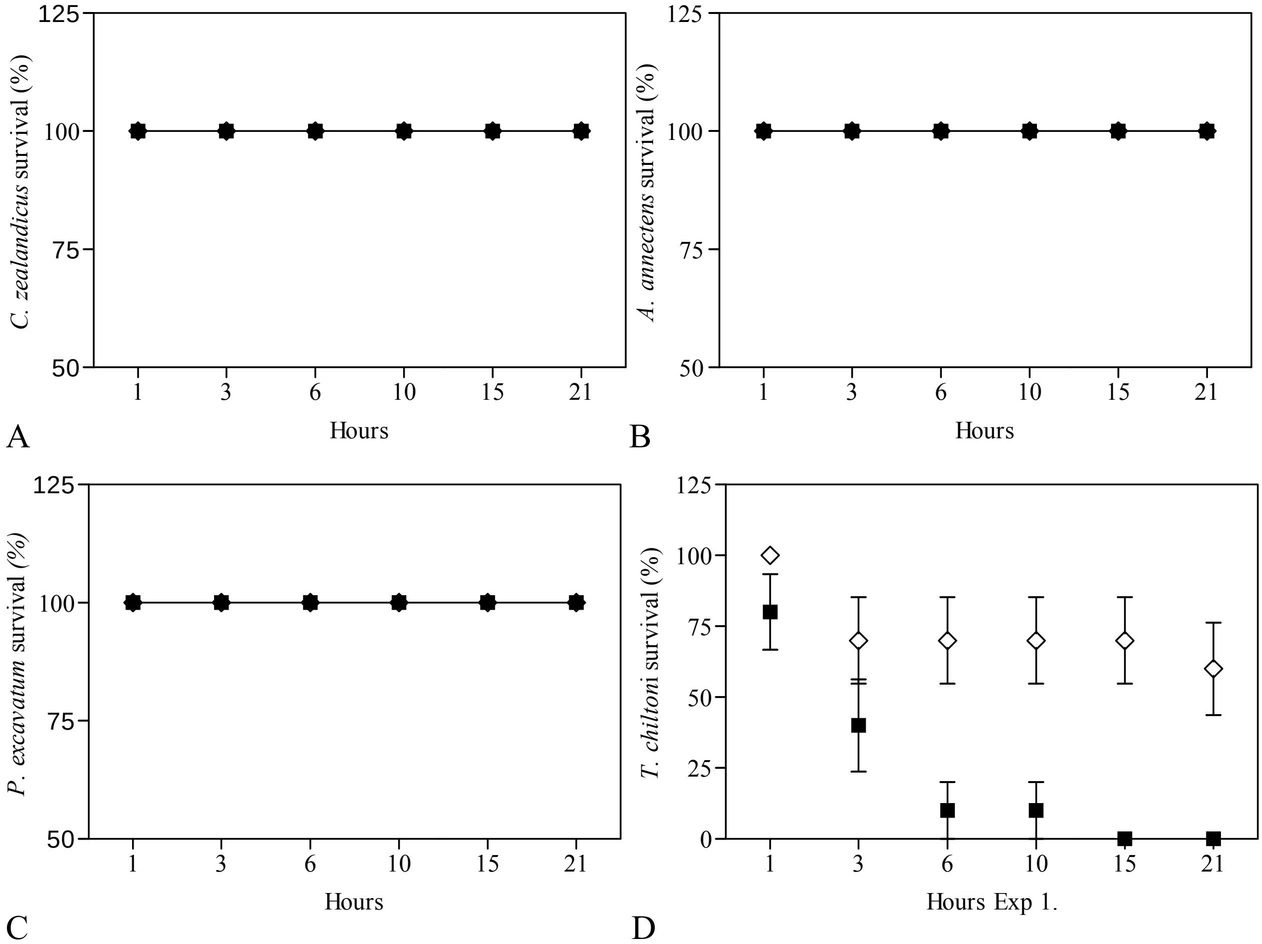


Figure 4.3 The relationship between survival and drying time at 25 °C (■)and 11 °C (◊). Experiment 1: Dry for 1, 2, 3, 4, 5, 6 hrs at a time with 5 minutes wet in-between. A) *C. zealandicus*. B) *A. annectens*. C) *P. excavatum*. D) *T. chiltoni.*

Experiment two

- Short term drawdown: 6 hrs dry, 10 minutes wet, 6 hrs dry.

Two of the four invertebrates, *C. zealandicus* and *A. annectens,* survived over the two 6 hr dry periods, irrespective of temperature (Figure 4.4). All *P. excavatum* survived at 11 °C, however, survival was reduced at higher temperatures (25 °C; Figure 4.4). There was a significant interaction effect (Two-way ANOVA, $F_{2,54} = 13.5$, $P < 0.0001$) between both temperature ($F_{1,54} = 13.5$, $P = 0.0005$) and time exposed ($F_{2,54} = 13.5$, $P < 0.0001$). Temperature had a significant effect on *P. excavatum* after 12 hrs (Bonferroni post-hoc tests, $t = 6$, $P < 0.001$), whereas, *T. chiltoni* survival decreased after 6 hrs (Figure 4.4). Two-way ANOVA showed a significant interaction effect ($F_{6,126} = 2.62$, $P = 0.019$) between both temperature ($F_{1,54} = 16$, $P = 0.0002$) and time exposed ($F_{2,54} = 32$, $P < 0.0001$) on *T. chiltoni* survival. Temperature had a significant effect after 6 hrs and 12 hrs (Bonferroni post-hoc tests, $t = 4.16$, $P < 0.001$; $t = 2.77$, $P < 0.05$ respectively).

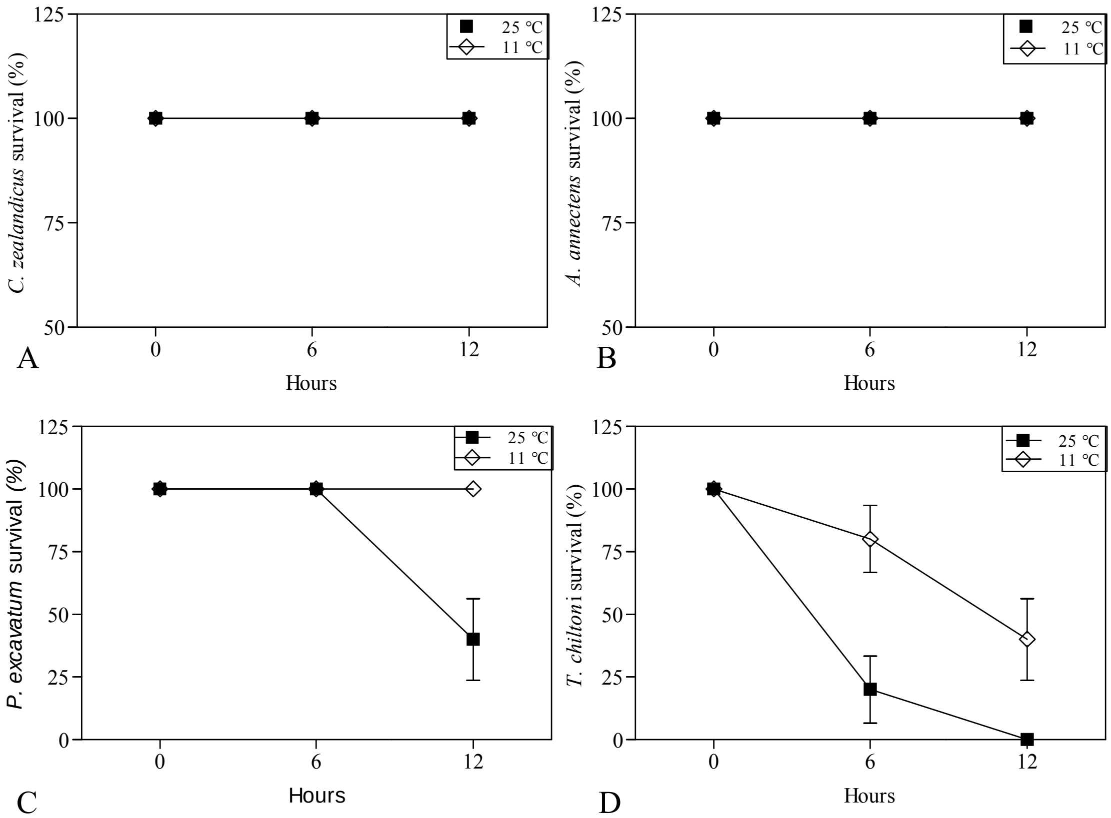


Figure 4.4 The relationship between survival and drying at 25 °C and 11 °C. Experiment 2: Dry 6 hrs, wet 10 mins, dry 6 hrs. A) *C. zealandicus.* B) *A. annectens.* C) *P. excavatum.* D) *T. chiltoni.*

Experiment three

- Long term drawdown: 24 hrs dry
- Immersion: 24 hr wet

C. zealandicus individuals survived for 24 hrs at both temperatures under dry conditions. *A. annectens* survived all treatments, except for 24 hrs dry at 25°C. Two-way ANOVA showed no significant difference between dry and wet treatments or effect of temperature. However, Bonferroni post-hoc tests showed a significant difference in *A. annectens* survival when dry between 25 °C and 10 °C ($t = 2.7$, $P < 0.05$). Survival of *P. excavatum* decreased at higher temperatures. Two-way ANOVA showed a significant interaction effect ($F_{1,36} = 81$, $P < 0.0001$) between temperature ($F_{1,36} = 121$, $P < 0.0001$) and water state (wet/dry; $F_{1,36} = 81$, $P < 0.0001$). Survival of *P. excavatum* was significantly lower in dry treatments at 25 °C (Bonferroni post-hoc test: $t = 14.1$, $P < 0.001$). Survival of *T. chiltoni* after 24 hrs decreased significantly in dry treatments compared to wet ($F_{1,36} = 361$, $P < 0.0001$) irrespective of temperature.

4.4.2 Invertebrate response to predation pressure

During predation experiments, temperatures in the tanks ranged between 15 and 18.5°C, with dissolved oxygen concentrations between 7.5 and 9 mg/L. There was no significant change in temperature or dissolved oxygen concentrations over the duration of the experiments.

Predation on the dragonfly, *P. grayi* was not affected by water clarity or the presence/absence of macrophytes (Figure 4.5). However, predation pressure may have been influenced by the size of fish predators compared to the dragonflies, as the smallest dragonflies (10-12 mm in length) were consumed, but few of the larger larvae were. Water clarity did not have any effect on survival of dragonfly larvae (Two-way ANOVA, $F_{1,36} = 0.342$, $P = 0.562$; Figure 4.5). Predation pressure on larvae of the damselfly *X. zealandicus* was not influenced by water clarity (Two-way ANOVA; $F_{1,36} = 0.3$, $P = 0.56$) or on the survival of *A. wakefieldi* (Two-way ANOVA, $F_{1,36} = 0.569$, $P = 0.45$). In contrast, predation pressure on the waterboatmen, *S. arguta* was lower in turbid water than clear water treatments (Two-way ANOVA $F_{1,36} = 11.07$, $P < 0.002$; Figure 4.5). In the presence of artificial plants, survival of the damselfly *X. zealandica* was significantly improved, with over 60% survival (Two-way ANOVA $F_{1,36} = 41.4$, $P < 0.0001$; Figure 4.5). *X. zealandicus* survival was significantly improved when macrophytes were present in both clear and turbid water treatments (Bonferroni post-hoc test, $t = 3.585$, $P < 0.001$; $t = 5.236$, $P < 0.001$; Figure 4.5). Survival of *Anisops wakefieldi* and *Sigara arguta* was not significantly influenced by presence of plants, irrespective of water clarity (Two-way ANOVA, $F_{1,36} = 0.320$, $P = 0.575$; $F_{1,36} = 1.876$, $P = 0.179$; Figure 4.5).

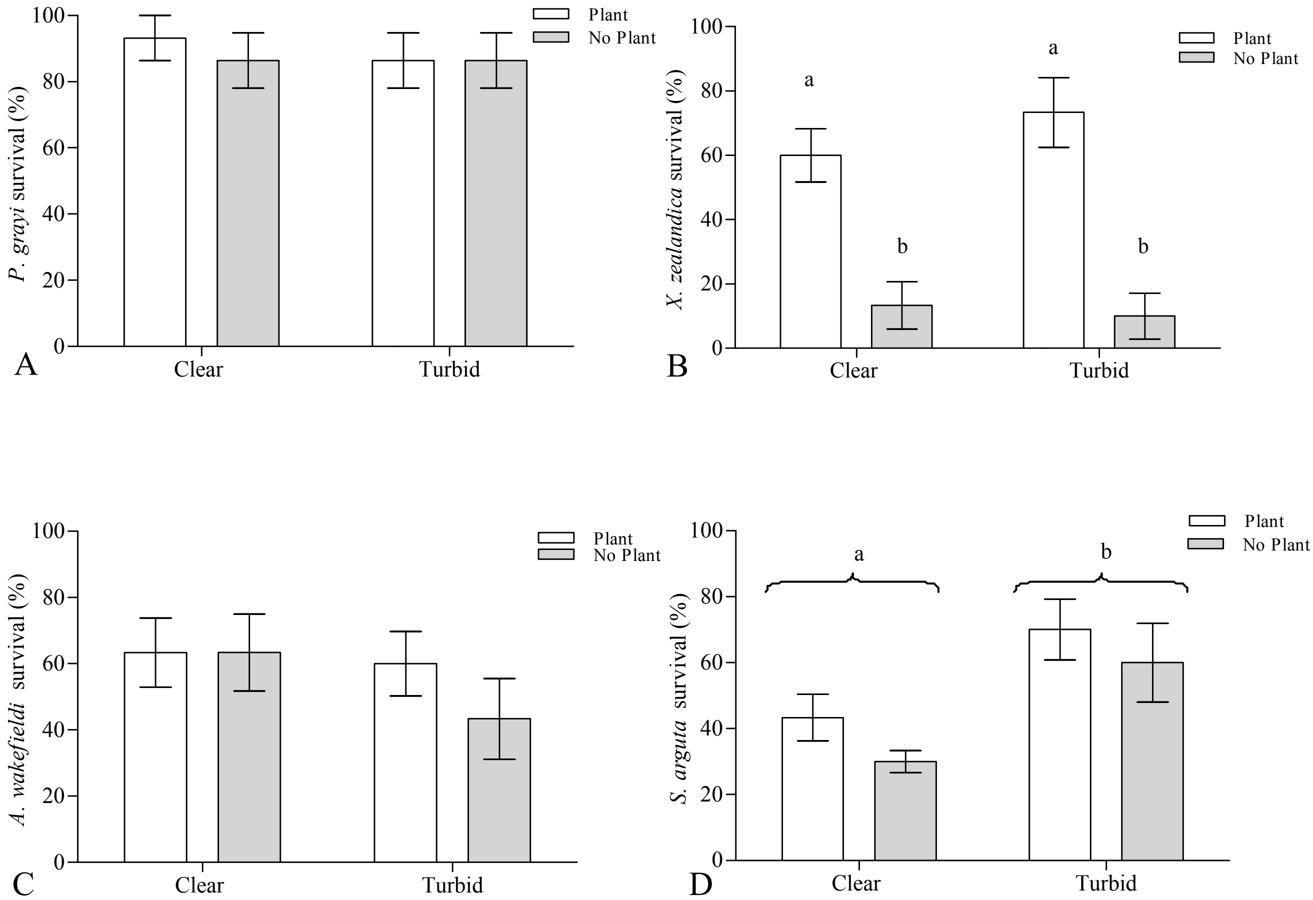


Figure 4.5 Survival of predatory invertebrates in four treatments with a predatory fish the common bully (n = 30, mean ± 1 SE) after 7 days. Significant differences are shown by letters above each bar. A) Dragonfly larvae, *P. grayi* (n = 15); B) Damselfly larvae, *X. zealandica*; C) Backswimmer, *A. wakefieldi*; D) Waterboatmen, *S. arguta*.

4.4.3 Do predatory invertebrates tolerate different saline concentrations?

Changing salinity had a significant effect on overall survival of benthic taxa. Combined survival rates of the damselflies *Xanthocnemis zealandica* and *Austrolestes colensonis*, the dragonfly, *P. grayi*, the backswimmer *A. wakefieldi*, the waterboatmen *S. arguta*, the midge *C. zealandicus* and the mysid shrimp *T. chiltoni* showed a significant non linear response with increasing salinity ($r^2 = 0.6$, $p < 0.001$) (Figure 4.6).

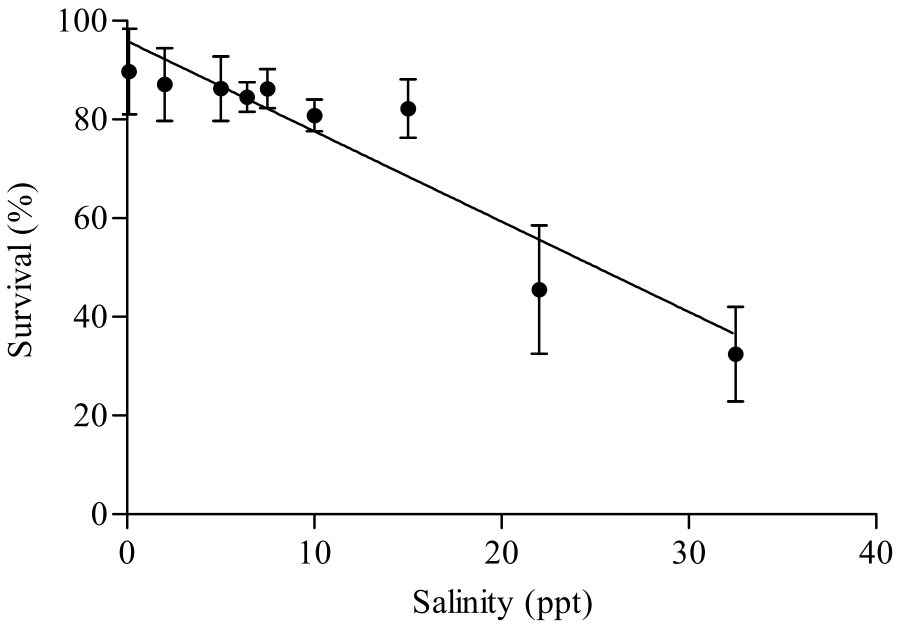


Figure 4.6 The relationship between survival and salinity of six benthic invertebrates (grouped) over 96 hrs (mean ± 1SE). Taxa included; *X. zealandica, A. colensonis*, *P. grayi*, *A. wakefieldi*, *S. arguta, C. zealandicus* and *T. chiltoni*.

All dragonfly larvae, survived in concentrations from freshwater (0.1 ppt) to brackish water (15 ppt) over 96 hrs (Figure 4.7). However, within the first 24 hrs in seawater (32.5 ppt), they all perished (Figure 7). A significant interaction (Two-way ANOVA, $F_{24,315,} = 4.883e+015$, $P < 0.0001$) of both salinity ($F_{6,315} = 7.813e+016$, $P < 0.0001$) and time exposed ($F_{4,315} = 4.883e+015$, $P < 0.0001$) was found. Dragonfly larvae survival was significantly higher in freshwater (0.1 ppt) than sea water (32.5 ppt) after 24 hrs (Bonferroni post-hoc test, t = 3, $P <$ 0.05).

The two damselfly larvae, *X. zealandica* and *A. colensonis* survived in most saline concentrations (Figure 7). Over the 96 hr period all damselflies survived in concentrations from 0.1 – 15 ppt, whilst 60% survived in pure seawater (32.5 ppt; Figure 4.7). However, almost half the individuals in concentrations from 5 – 15 ppt moulted three days after exposure, possibly as a result of physiological stress. A significant effect of salinity on damselfly survival was found (Two-way ANOVA, $F_{7,360} = 16.2$, $P < 0.0001$), but no effect of time.

In contrast to the odonate species, backswimmer survival was reduced in salinities > 5 ppt and time exposed to those concentrations (Figure 4.7). Two-way ANVOA showed a significant interaction ($F_{28,360} = 4$, $P < 0.0001$) of both saline concentration ($F_{7,360} = 53.5$, $P < 0.0001$) and time exposed ($F_{4,360} = 13.8$, $P < 0.0001$). Bonferroni post-hoc tests showed a significant effect of 5 and 10 ppt concentrations after 96 hrs (t = 2.9, $P < 0.05$), 15 ppt concentration after 48 hrs (t = 2.9, $P < 0.05$) and 35 ppt concentration after 24hrs (t = 6.7, $P < 0.001$) compared to survival in freshwater (0.1 ppt). Similarly, survival of the water boatmen, *S. arguta* was reduced at salinities above 15 ppt and time exposed to those concentrations (Figure 4.7). Two-way ANOVA showed a significant interaction ($F_{32, 405} = 8.9$, $P < 0.0001$) between both salinity ($F_{8, 405} = 77.5$, $P < 0.0001$) and time exposed ($F_{4, 405} = 29.4$, $P < 0.0001$). Bonferroni post-hoc tests show a significant effect of higher salinities compared to freshwater (0.1 ppt); 15 ppt concentrations after 48 hrs (t = 3.1, $P < 0.05$), 22 ppt after 72 hrs (t = 10.22, $P < 0.001$) and 32.5 ppt concentrations after 24 hrs (t = 10.22, $P < 0.001$).

Salinity tolerances of two taxa, which were common in Lakec Ellesmere were also tested. The chironomid, *C. zealandicus*, had its highest survival in weakly brackish water, but as salinity increased above 10 ppt, survival decreased (Figure 4.7). Two-way ANOVA showed a significant interaction effect ($F_{32,405} = 3.4$, $P < 0.0001$) between both salinity ($F_{8, 405} = 44.2$, $P < 0.0001$) and time ($F_{4,405} = 26.4$, $P < 0.0001$). Bonferroni post-hoc tests showed a significant effect of higher salinities; 10 ppt concentrations after 96 hrs and 15 ppt concentrations after 72 hrs (t = 2.98, $P < 0.05$; t = 2.98, $P < 0.05$), 22 ppt and 32.5 ppt concentrations after 24 hrs ($t = 4.46$, $P < 0.001$; $t = 7.44$, $P < 0.001$, respectively). Survival of the mysid shrimp, *T. chiltoni* was lowest in freshwater and seawater treatments and was highest in brackish water (Figure 4.7). Two-way ANOVA showed a significant interaction effect ($F_{4,405} = 2.4$, $P < 0.0001$) between both salinity ($F_{8, 405} = 9.6$, $P < 0.0001$) and time ($F_{4,405} = 73.6$, $p < 0.0001$). Bonferroni post-hoc tests showed a significant effect of freshwater on survival after 72 hrs compared to all salinities higher than 2 ppt ($t = 4.49$, $p < 0.001$), 5 ppt ($t = 5.24$, $P < 0.001$), 6.4 ppt ($t = 4.49$, $P < 0.001$), 7.5 ($t = 3.74$, $P < 0.01$), 10 ppt ($t = 5.99$, $P < 0.001$), 15 ppt ($t = 5.24$, $P < 0.001$) and 22 ppt ($t = 5.24$, $P < 0.001$). No significant difference was observed between the survival of *T. chiltoni* in fresh water or seawater.

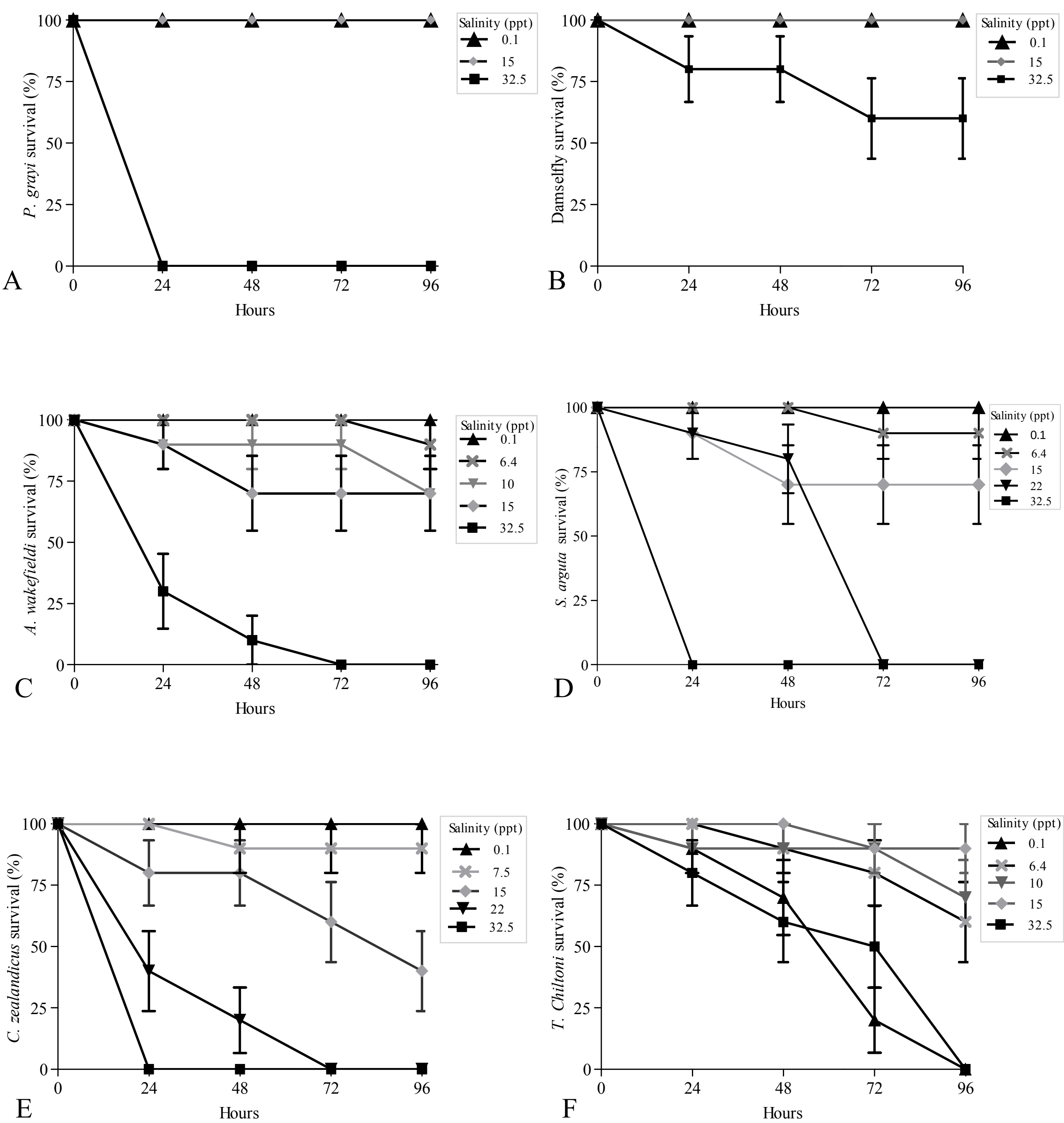


Figure 4.7 Survival rates of benthic invertebrates over 96 hrs at 15°C in saline concentrations ranging from freshwater to seawater (n=10, SE); A) Dragonfly larvae (*P. grayi*), B) Damselfly larvae, *X. zealandica* and *A. colensonis*), C) Backswimmer, *A. wakefieldi*, D) Water boatmen *S. arguta,* E) Midge, *C. zealandicus,* F) Mysid, *T. chiltoni*. Note: Saline concentrations have been omitted from graphs when survival was the same**.**

4.5 Discussion

My experiments indicate that extended water level drawdown, would have significant impacts on the survival of a number of lake taxa, assuming they could not move away (down) with decreasing water levels. Thus, whilst members of the benthic fauna of Lake Ellesmere/Te Waihora appear to be adapted to frequent episodes of water level change their responses are dependent on temperature and total time spend dry. The results from my mesocosm experiments indicate that multiple factors may be responsible for the absence of predatory invertebrates in Lake Ellesmere/Te Waihora. Predation pressure, mediated by the absence of macrophyte refugia and turbidity affected the damselflies and water boatmen, respectively. Salinity may be affecting the recruitment of some predatory invertebrates (e.g., *Anisops wakefieldi*), but is clearly not the primary causal factor for the absence of all predatory invertebrate species.

4.5.1 Effects of lake level fluctuation

The strongest differences in the invertebrate species currently inhabiting the littoral zone of Lake Ellesmere/Te Waihora were found between those that inhabit sediments and those that reside in the water column. Despite all taxa being dominant members of the lake community, significant differences in desiccation resistance were observed (Figure 4.3 & 4,4). This was expected, as species such as *C. zealandicus* generally burrow in the sediment, whereas *T. chiltoni* does not burrow, but is more mobile and inhabits the water column in the mid-littoral- to lower littoral zone. Survival of invertebrates in the desiccation experiments, irrespective of temperature was improved in the presence of sporadic re-wetting. This suggests short-term fluctuations in water level in the lake are important inundation events and provide opportunity for more mobile species such as *T. chiltoni* and *P. excavatum* to escape drying conditions (if stranded) and replenish moisture to burrowing invertebrates such as *C. zealandicus*. *Austridotea annectens* appeared to be very tolerant of environmental conditions and well adapted to the dynamic nature of the lake. It is able to burrow when exposed to desiccation but, is also mobile, allowing escape during water drawdown and when water levels increase. Results suggest that the most detrimental impact of water level drawdown on benthic invertebrate survival would occur over summer when temperatures and rates of evaporation are high, and episodes of re-wetting are less frequent. Rapid drawdown of lake level during opening events, for longer than 24 hrs, generally occurs over winter months when lake levels are high, due to rain and flooding events (Hayward 2009). This rapid drawdown is likely to leave some invertebrates 'high and dry'. However, cooler temperatures may permit individuals to survive until water levels rise. On the other hand, slower water level decline over summer, driven largely by warmer temperatures and evapotranspiration, as well as reduced tributary inputs, may provide the opportunity for benthic invertebrates such as *P. excavatum* to respond and escape. However, individuals experiencing desiccating conditions at warmer temperatures are less likely to survive. The extent and duration of drawdown coupled with the time of year are therefore very important drivers of benthic invertebrate survival in Lake Ellesmere/Te Waihora.

4.5.2 Influence of predation pressure

Predation pressure can be an important factor controlling species composition in aquatic environments (Brooks & Dodson 1965; Wellborn *et al*. 1996). In many freshwater systems fish represent the top predators (Wellborn *et al*. 1996). Therefore, composition of the fish community may in-turn affect the composition of the invertebrate community (Wettwer *et al.* 2010). In New Zealand, the common bully, *Gobiomorphus cotidianus* is widely distributed in lakes (McDowall 1990) and is the most abundant fish species in Lake Ellesmere/Te Waihora, comprising 92% of the fish community (Kelly & Jellyman 2007). The common bully is a small endemic fish that generally occupies the littoral zone (McDowall 1990; Rowe 1999), where it preys on a variety of invertebrates and might be expected to have a large impact on predatory invertebrates (Forsyth et al 1990; Rowe *et al.,* 2001).

Predation rates in turbid water are often higher than in clear water, as prey become more active and anti-predator prey strategies become less effective (Abrahams & Kattenfeld 1997). However, it is harder for fish to see prey in turbid waters, so in other instances predation is lower in turbid water (Boner & Wilde 2002). Consequently, invertebrate community structure can significantly differ between clear and turbid water states as a result of fish predation (Van de Meutter *et al.,* 2005). Results from my predation experiments showed that water state had relatively little impact on predation rates by *G. cotidianus* on three of the four prey taxa offered (damselflies, dragonflies and backswimmers) (Figure 4.5). Survival of the waterboatmen, however, declined in clear water, irrespective of macrophyte presence. Other studies have shown predation rates of fish on other Corixidae (waterboatmen) species to be high, causing them to become locally extinct irrespective of macrophyte presence (Oscarson 1987). Observed differences between the survival of prey taxa in my experiments may have been related to species behavioural traits, specific predator avoidance traits, such as reduced locomotive activity (Sih 1982; McPeek 1990) or predator/prey size ratios (Gill 2003). It is probably not surprising that predation rates on backswimmers were higher than on waterboatmen. Although, both species use a plastron to stay submerged by trapping air in pockets at the tip of the abdomen, backswimmers generally sit in the water column as opposed to water boatmen which attach themselves to plants or other substrates (Oscarson 1987), leaving backswimmers more exposed to fish predation. Predation on benthic invertebrates is influenced by gape size of the predator (fish), which will influence how large a prey items it can consume (Gill 2003). Dietary analysis on common smelt (*Retropinna retropinna*) and shortfin eel (*Anguilla australis*), two other abundant predatory fish in Lake Ellesmere/Te Waihora showed that they consume larger prey species than does *G. cotidianus* (Kelly & Jellyman 2007). Both *A. wakefieldi* and *S. arguta* are particularly vulnerable to predation during vertical migration to the surface to replenish air supply. However, presence of macrophytes did not seem to improve the survival of backswimmers or water boatmen (Figure 4.5). Perhaps if taller plants had been used, survival would have been greater.

Predation pressure resulting from the absence of macrophyte refugia in Lake Ellesmere/Te Waihora seems most likely to inhibit the establishment of dragonflies and damselflies. My results suggested that small dragonfly instars (< 12 mm) were most vulnerable to predation by medium to large *G. cotidianus*. Furthermore, whilst collecting dragonfly larvae from Lake Sarah I observed that the smallest nymphs occurred towards the centre of dense vegetation patches, as opposed to the larger more developed nymphs, which were generally collected on the outer edges of vegetation beds. Other studies have also found that macrophyte structure and type is important for odonate presence. For example, Remsburg & Turner (2009) found that the presence of tall macrophytes was significantly correlated with damselfly and dragonfly richness and abundance in other lake systems. Other studies have found dragonfly diversity to differ significantly between lakes with and without fish, and that the presence of macrophytes increased their presence (McPeek 1990; Johansson *et al*., 2006). Feeding behaviour and anti-predator strategies are also likely to influence survival and can be a major constraint on species attempting to co-occur with fish (Johnson 1991; Wissinger *et al.,* 2009-2028). For example, some damselflies, like *X. zealandica*, are sit and wait predators that favour macrophytes as resting habitat, others stalk their prey and are mobile and thus, run a greater risk of being caught by fish. In the presence of predators, damselfly species often adjust their behaviour and become less active. However, some species are not able to adjust their behaviour to the threat of predation (Henrikson 1988) and therefore, do not co-occur with a certain predator (Wittwer *et al*., 2010). More active damselfly species are liable to be more susceptible to encounters with fish predators than those that are not. Invertebrates in open water are likely to be more exposed to visual predators, such as the common bully than species in habitats with sheltering vegetation. Thus, macrophytes and predation pressure appear to play a key role in determining the presence of Odonata in lake ecosystems.

4.5.3 Salinity

Salinity had a significant effect on the overall survival of benthic taxa in my experiments, with increasing saline concentrations negatively affecting survival of several taxa that currently inhabit the lake and some that do not. This suggests, as others have found abroad, that invertebrate taxonomic richness decreases as salinity increase in estuarine conditions (Kefford *et al*., 2003; Ellis & Macisaac 2009). The absence of odonate species (e.g., *X. zealandica*, *A. colensonis* and *P. grayi*) from Lake Ellesmere does not seem to be due entirely to salinity, as these taxa were able to survive concentrations from freshwater up to 15 ppt. In seawater, damselfly survival declined slowly over 96 hours, whereas dragonfly larvae generally died within 24 hrs. Prior to mortality, individuals showed signs of stress as salinity increased, such as reduced mobility and increased moulting. It is not known how salinity affects earlier life stages such as egg development of these particular species. However, studies on other damselfly species such as *Ischnura heterosticta* over a longer time period (21 days to 4 months) suggest growth and development were optimal in brackish water between 3 and 10 ppt, with damselflies dying after long term exposure to concentrations > 18 ppt (Kefford *et al*., 2006). It is possible that at higher salinities, swimming performance of some species may be affected (Harris & Morgan 1984), and that predation on them is enhanced when suitable refuges are rare. Furthermore, salinity has been shown to affect the type of vegetation that might further influence habitat selection (Thorp & Covich 1991) and water levels that are constantly in a state of flux have been shown to have particularly negative effects on Odonata egg development (Corbet 1962). If *X. zealandica* and *A. colensonis* physiology is similar to that of *I. heterosticta* then salinity is not likely to be a factor restricting population establishment in Lake Ellesmere/Te Waihora. This is further supported by the presence of odonates in Waituna Lagoon, a coastal brackish lagoon, South Island, New Zealand (Moore 1989).

Backswimmers and waterboatmen have many characteristics in common; both inhabit still-waters especially ponds/lakes and stagnant pools. Backswimmers are predatory, feeding on insect and other animal life in the water and water boatmen are omnivorous. Backswimmers and waterboatmen both showed a significant decrease in survival when exposed to increasing saline concentrations over time. However, the survival of *S. arguta* was significantly reduced in seawater over a shorter time period than *A. wakefieldi*. Both species survival was highest in freshwater at low brackish water concentrations (0.1 – 6.4 ppt), indicating some tolerance and ability to persist in intermittently brackish conditions. However, like damselfly and dragonfly larvae, they are not currently found in the lake and the ability of these taxa to survive long-term in brackish water is not known.

At Kaituna Lagoon, at the south-east end of Lake Ellesmere/Te Waihora, a semi-permanent pond separated from the lake by a 1 m buffer strip of vegetation (which during high lake levels overflowed into the pond), was found to contain abundant populations of three of the four predatory invertebrate species used in my experiments; *X. zealandicus*, backswimmers and waterboatmen. Water quality was poor, with low dissolved oxygen concentrations, anoxic bottom sediments and higher salinity (by 1 ppt) than the lake (presence of fish predators was unknown). The primary difference between the two water bodies was the occurrence of submerged macrophytes, emergent vegetation and the absence of frequent water level fluctuations. Therefore, results from my experiments combined with the presence of predatory invertebrates in immediate proximity to the lake, suggests lack of macrophytes might be the primarily reason for the absence of predatory invertebrates in the lake.

Another possible factor for the lack of invertebrate predators in Lake Ellesmere/Te Waihora, could be the frequent fluctuations in water level and intense wave action that occurs in the littoral zone (Diehl, 1992). Invertebrate predators such as dragonfly and damselfly larvae tend to prefer slow-moving or lentic waters with macrophytes present (Kadoya *et al*. 2004) as observed in the semi-permanent pond in Kaituna Lagoon. Therefore, moderate wave action may be unsuitable for these predators. However, other wind-affected lakes such as Grasmere and Sarah in inland Canterbury, support the invertebrate predators, *P. grayi, X. zealandica, Cura pinguis* and *Glossiphonia multistriata* (Timms 1982), and all have submerged and emergent vegetation.

C*hironomus zealandicus* and the mysid shrimp *Tenagomysis chiltoni* are common littoral zone invertebrates of the lake and constitute significant proportions of fish diets in the lake (Ryan 1986; Sagar *et al.* 2004; Kelly & Jellyman 2007). Results from my salinity experiments showed differences in survival between the two species. *C. zealandicus* survival was best in salinity concentrations up to 7.5 ppt but, longer exposure to concentrations > 15 ppt significantly decreased survival. Conversely, survival of *T. chiltoni* was significantly reduced over time in freshwater and seawater concentrations over the 96 hrs. Survival was significantly higher in brackish salinities. Although *C. zealandicus* can burrow into bottom sediment to effectively protect itself, salinity experiments suggest they might be vulnerable to short term (< 24 hr) increased salinity, which frequently occurs when the lake is opened. Although *T. chiltoni* populations can tolerate higher brackish salinities than *C. zealandicus*, they could potentially be impacted during extended periods of very high or low lake salinity levels, in accordance with their inverted 'U'-shaped concentration-response curve (Clark *et al*., 2004; Chapter 3). Such extreme conditions may occur over winter when the lake is unable to be opened, or alternatively, if the lake is open for extended periods.

4.5.4 Summary

The duration of drawdown coupled with the time of year appear to be important drivers of benthic invertebrate survival in Lake Ellesmere/Te Waihora. The current water level opening regime and trigger levels primarily result in the lake being opened during winter months and consequently, should have less detrimental impacts on benthic fauna than openings over summer. The benthic community seem to be well adapted to the dynamic nature of the littoral zone, particularly those inhabiting bottom sediments, which can withstand longer periods of dewatering when infrequently inundated by water. Periods of inundation are important for those species that usually reside in the water column, but become stranded when dewatering occurs, as it allows them a chance to escape when water returns. High predatory fish biomass and lack of macrophytes, coupled with salinity in the lake creates an unfavourable environment for predatory invertebrates. However, as predatory invertebrates are found in other lake systems with high fish abundance, in other brackish lakes and in close proximity to the lake itself (Kaituna Lagoon pond), the absence of macrophytes may be the primary factor inhibiting predatory invertebrate presence in the lake. Furthermore, fluctuating water levels and high turbidity in the lake create an unfavourable environment for re-establishment of macrophyte beds. The lake is a complex system. If improving Lake Ellesmere/Te Waihora water quality and biodiversity are to be achieved, the first priority should be to reduce external and internal nutrient loads, with a long term goal being to re-establish macrophytes.

Chapter 5

General Discussion

5.1 General Discussion

The littoral zone of lakes are generally characterised by a mosaic of habitat types, which supports high biological diversity (Benson & Hudson 1975; Menge & Lubchenco 1981; James *et al*., 1998; Scheifhacken *et al.,* 2007; de Mendoza & Catalan 2010). Typically the littoral zone is also the most productivity zone in a lake, much higher than the pro-fundal zone (Tolonen *et al*., 2001). However, anthropogenic activities are increasingly altering riparian areas and littoral zones for shoreline development and agricultural activities, which impact the structure, hydrology and water quality of lakes. The ecological impacts of these anthropogenic activities have rarely been quantified in New Zealand. Particularly, invertebrate assemblages in the littoral zone of shallow brackish lakes have been largely neglected. The response of benthic invertebrates to environmental variables such as water level and salinity fluctuations are, therefore, no where nearly as well understood as one might expect. Improving this knowledge is essential in understanding and assessing how human alterations such as manual lake openings, impact the structure, function and productivity of invertebrate communities in the littoral zone and therefore foodwebs throughout the whole lake.

5.1.1 Importance of the littoral zone for primary and secondary production

Twenty eight taxa were recorded in the eulittoral zone during this study, which is higher than recorded in the lake previously (Ryan 1986; Dawn 1995, Sagar *et* al., 2004; Kelly & Jellyman 2007; Wood 2008). Four taxa dominated (95%) invertebrate composition; *P. excavatum*, oligochaeta, *C. zealandicus* and *P. antipodarum*. Another four taxa were recorded widely, but in low numbers (*A. annectens,* Ostracoda, polychaeta and *T. chiltoni*). Taxonomic richness in New Zealand lakes is considered low compared to other lands in the South Pacific (Stout 1975; Timms 1982). However, Lake Ellesmere/Te Waihora has similar taxon richness to that of other inland lakes in New Zealand (Mylechreest 1978; Biggs & Malthus 1982). Mylechreest (1978) recorded twenty six macroinvertebrate taxa in the littoral zone of the oligotrophic Lake Waikaremoana, while Talbot & Ward (1987) found similar numbers in macrophytes beds in Lake Alexandrina, a mesotrophic lake, and Biggs & Malthus (1982) recorded twenty six taxa in lakes of the upper Clutha Valley. In contrast, James *et al*., (1998) recorded high taxon richness, forty seven taxa in the littoral zone of Lake Coleridge (a large oligotrophic lake), and Sanders (1996) recorded fifty four taxa in the river deltas flowing into the Waitaki lakes. As with Lake Ellesmere/Te Waihora, many lakes in New Zealand appear to be dominated by 3 - 5 invertebrate taxonomic groups. Furthermore, Timms (1982) suggests species diversity in New Zealand lakes is not related to water quality (trophic state), but rather the influence of other factors, such as presence of macrophytes and suggests that low species richness is associated to extreme environments, such as turbid glacial melt-water or high sedimentation rates and that high species richness will occur in lakes with a large allocthonous input. However, Lake Ellesmere/Te Waihora is probably one of the most extreme lake environments, with an altered hydrological cycle, fluctuating salinity regime and high sedimentation. The higher number of taxa in Lake Ellesmere/Te Waihora suggests that even though the water quality is degraded and lake levels are constantly changing, there are a broad range of habitat niches available for benthic invertebrates.

Within the littoral zone abundance and diversity of invertebrates was highest in the eulittoral region. The mid-littoral and lower littoral zones had lower taxon richness and densities and were generally similar in composition. The less mobile molluscs, *P. antipodarum* were a dominant component of benthic community in the eulittoral zone (30%), with significantly lower abundance in the mid-littoral and lower littoral zones. Oligochaetes and *C. zealandicus* were found to be the stable taxa of benthic community in the lake, occurring throughout the lake with generally even distributions across the littoral zone. The more mobile crustaceans (i.e. *P. excavatum* and *T. chiltoni*) were dominant in the mid-littoral to lower littoral zone. As with other studies in New Zealand, seasonal changes in invertebrate dominance were observed in relation to life cycles (Winterbourn 1970; James *et al*., 1998). In Lake Ellesmere/Te Waihora the mollusc *P. antipodarum* showed a summer peak (February) in densities along the littoral zone. In the eulittoral zone a slow decline in density was observed over the preceding 7 months, from summer (46%), autumn (34%) to winter (23%). In contrast, *C. zealandicus* densities were found to increase from summer (3%) to winter (34%). However, summer sampling may have been after mass emergent events and, therefore may not be an accurate representation of midge densities. Seasonal variation in invertebrate composition was less varied in the mid-littoral and lower littoral than the eulittoral zone and likely indicates a strong influence of physical disturbance, particularly water level fluctuations. Baumgärtner *et al.,* (2008) found benthic invertebrate communities to differ along the littoral zone depth gradient as a result of different dominant structures. They found invertebrate diversity to be related to habitat diversity, with the eulittoral zone having high habitat (i.e. tree roots, stones, woody debris) and invertebrate diversity, both decreasing and becoming more homogonous the further out into the lake. Furthermore, Brauns *et al*., (2008) suggests that loss of eulittoral habitat will cause a significant alteration of the littoral invertebrate community and have flow on impacts on higher trophic levels.

The littoral zone represents a relatively large area of Lake Ellesmere/Te Waihora, and these data suggest that invertebrate numbers within this zone are vitally important to the functioning of the lake (James *et al.,* 2000; Kelly & Jellyman 2007). Even in large, deep lakes where the littoral zones represent a small proportion of lake area, the littoral zone still plays an important role in whole-lake processes (Scheifhacken *et al*., 2007). The eulittoral zone in Lake Ellesmere/Te Waihora is therefore, likely to be vitally important to the lakes energy production and food-web ecology. Both Kelly & Jellyman (2007) and Wood (2008) showed benthic invertebrates (i.e. molluscs *P. antipodarum*, the midge *C. zealandicus* and oligochaetes) to constitute a significant proportion of juvenile eel (*Anguilla australis*), common bully (*Gobiomorphus cotidianus*) and common smelt (*Retropinna retropinna*) diets. Although I did not address the link to levels of primary productivity, the higher solar irradiance and temperatures in shallow waters may be responsible for enhanced algal and phytoplankton growth. The littoral zone in the lake is also frequented by large numbers of birds (O'Donnell 1989) and invertebrates are likely an important source of food to these extensive populations. However, this zone is one in which the consequences of various types of human disturbance including, agricultural intensification, increased water abstraction, reduced tributary inflow and lake opening events might be become more apparent.

5.1.2 Effects of environmental variables on invertebrate composition in the littoral zone

In this study, the variability in both density and taxonomic richness in the benthic invertebrate community along the littoral zone was correlated with changes in abiotic parameters both spatially and temporally. The lake is exposed to significant shifts in water level over seasonal and daily scales. This shift has the potential to impact invertebrate assemblages over the period of hours to days, whereas seasonal differences in freshwater and saltwater inputs have the potential to affect lake flora and fauna over longer time scales. This was demonstrated by seasonal shifts in species compositions within sites. Temperature variation between seasons had a large effect on species diversity and abundance. In particular, the combination of water level fluctuations and high temperatures during summer may have an impact on desiccation and mortality of many invertebrates. Decreasing water levels, likely negatively affect benthic invertebrate densities (i.e. loss of trapped individuals) particularly in the eulittoral zone over summer when the risk of desiccation is higher (Mörtl 2003; Baumgärtner 2004). In contrast to decreasing water levels, benthic invertebrate communities in the eulittoral zone would benefit from increasing water levels as new habitat becomes available.

Generally, water level change was the dominant factor explaining seasonal variation over 2009, particularly in the eulittoral zone. Taxonomic richness increased in the eulittoral zone with increasing water level, most likely a result of increased habitat availability, while the mid-littoral and lower littoral remained relatively constant. A decrease in benthic invertebrate density within the eulittoral and mid-littoral zone were observed with increasing water level. Similarity, Palomäki (1994) observed littoral benthic invertebrate biomass to decrease with increasing water level fluctuation. Mörtl (2003) and Baumgärtner (2004) observed variation in drift-line samples and attributed this to water level fluctuations prior to sampling. The effects of increasing water levels were less pronounced in my study than decreasing water levels and are presumably responsible for the observed low densities observed over higher water levels where habitat was freshly submerged.

It is likely that benthic invertebrate composition and density in the lake was driven by a combination of water level change and associated water chemistry parameters. Unlike inland water bodies, Lake Ellesmere/Te Waihora is subject to large fluctuations in salinity due to marine inputs. This has the potential to be a major driver of the invertebrate community, as there is a limited number of aquatic species that can tolerate fluctuating saline concentrations (Figure 5.1). Therefore, major variations in salinity, either high or low, have the potential to negatively affect survival of lake flora and fauna (Remane 1934). Results from this research indicate large temporal differences in salinity (0.7 – 27 ppt) between the sampling sites in Lake Ellesmere/Te Waihora. This variation in salinity was associated with large differences in the density of invertebrates found at each site and resulted in a hump shape distribution, both in richness and density (Figure 3.10). Invertberate density was variable acoss the salinity gradient, but was generally lower at very low and high salinities. Spatial differences in composition and density suggests invertebrates in the lake are tolerant fluctuations in saline concentrations (Figure 5.1). Benthic invertebrates appear to be adapted to lower-mid range of salinities and fluctuations above or below this range can negatively affect the relative biomass and diversity of invertebrates (Figure 5.1). Furthermore, the duration of salinity increase, particularly at the higher end of the scale is likely to significantly impact invertebrate survival. As in many brackish water systems, taxa diversity is limited to species that are able to tolerate relatively large variations in salinity (Remane 1934). Although at any one time, salinity may be within the range of a number of species, the seasonal variation in salinity may have large effects on invertebrates adapted to a narrow range of salinity.

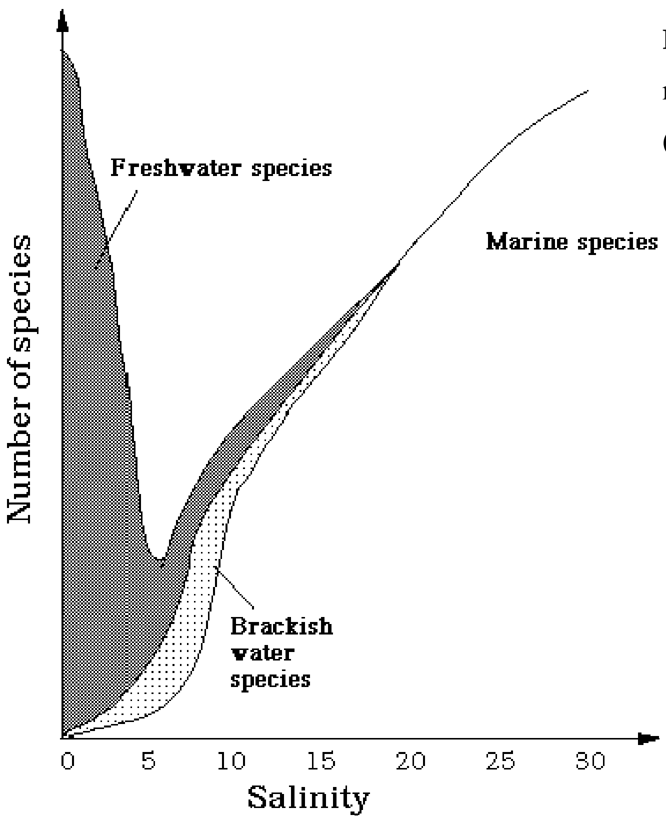


Figure 5.1 Relationship between salinity and number of species. Håkanson & Eklund (2010) re-drawn from Remane (1934).

Predatory invertebrates occupy an important position in lake foodwebs, where they are both predators of other invertebrates and a valuable prey resource of fish (Johnson 1991). However, Schallenberg & Waite (2004) noted that invertebrate predators have not been widely reported in our coastal lakes, compared to alpine lakes were they are relatively common (Crumpton 1977; Biggs & Malthus, 1982; Talbot & Ward 1987; Crumpton 1997. The lack of predatory invertebrates in Lake Ellesmere/Te Waihora is likely driven by multiple factors and interactions from water level fluctuation, salinity, coupled with predation pressure and lack of macrophytes for refuge and habitat. If invertebrate predators such as, damselfly (*X. zealandicus*), dragonfly (*P. grayii*) and water boatmen (*A. wakefieldi*) were present in the lake, they could have a large impact on *C. zealandicus* populations, reducing the magnitude of emerging adult swarms and their effect on local residents (Wood 2008). Furthermore, they would provide a higher energy food resource for fish in the lake and may help improve the declining growth rates of juvenile eels (Jellyman *et al*., 1998). My results show some fundamental links between salinity and survival of several predatory invertebrates. Furthermore, the lack of macrophyte beds and turbidity within the lake may be affecting predation dynamics, with very little refuge for invertebrate fauna. Future research on the ability of predatory invertebrates to withstand fluctuating water levels would provide additional knowledge and information on their tolerance to extreme environments.

5.1.3 Implications for management

High levels of nutrient runoff entering the lake directly influence phytoplankton productivity. This has resulted in a significant shift in the eutrophic state of the lake, and has compromised some of the aesthetic and possibly ecological qualities. Furthermore, the decreased inflows from the surrounding catchments may be concentrat nutrient concentraions. Alterations of the local hydrological regime in the lake's catchment have likely added to the degradation of water quality and biodiversity in Lake Ellesmere/Te Waihora. My data indicates that the current lake opening regime (open over winter) reduces the risk of benthic invertebrate communities being exposed to high reducing the risk of desiccation. Currently, lake opening events appear to have little impact on water quality and phytoplankton biomass, apart from increasing salinity in the lake. Based on results from this study, I suggest a minimum lake level be set at Taumutu of 0.6 m during the months from November – March in order to protect benthic invertebrate communities in the eulittoral zone from extensive loss of habitat, reduced temperature extremes, reduced risk of desiccation and improved survival. My findings suggest, that of the three proposed scenarios being currently proposed for lake management (Hughey 2009); scenario two, 'realistic and resilient' would be most achievable and beneficial to lake values. However, I believe that the addition of having a minimum water level of ~0.6 m for the proposed closing regime would provide better protection for the ecological community. This would allow lake opening events for fish migration in autumn and spring (before temperatures increase), providing the lake is closed and maintained at a minimum lake level of 0.6 m from November - March. Fish would also benefit from an increased water level by having more productive and diverse prey to select in the eulittoral zone, potentially improving fish growth rates and populations over summer. Having a minimum set at 0.6 m would provide sufficient littoral zone habitat for the lakes extensive bird life, providing both high availability of food and habitat for nesting and breeding. Furthermore, physical and chemical water quality properties would benefit from an increased water level over summer months, by reducing water temperatures, diluting readily available nutrient concentrations and potentially reducing phytoplankton (and potentially toxic cyanobacterial) blooms.

5.1.4 Summary

In conclusion, I have shown that the littoral benthic invertebrate community in Lake Ellesmere/Te Waihora varies spatially and temporally around the lake depending on water level and salinity. Benthic invertebrate communities are generally more diverse and productive in the upper most eulittoral zone. Therefore, anthropogenic activities which modify hydrodynamic and water quality conditions can potentially have a large negative impact on the structure and diversity of the littoral invertebrate community as well as flow on effects through the lake food web. This thesis provided a mechanistic understanding of how water level manipulation alters the relationship between environmental factors and benthic invertebrate communities in the littoral zone. This knowledge can be used in order to develop scientifically sound approaches to minimise impacts on benthic invertebrate communities in lake ecosystems.

References

Abrahams, M. V., & Kattenfeld, M. G., (1997). The role of turbidity as a constraint on predator prey interactions in aquatic environments. Behavioural Ecology and Sociobiology **40**:169-174.

Allan, J.C., & Kirk, R.M., (2000). Wind wave characteristics at Lake Dunstan, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research. **34**: 573-591.

ANZECC (Australian and New Zealand Environment and Conservation Council), (2000): Australian Water Quality Guidelines for Fresh and Marine Water. Australian and New Zealand Environment and Conservation Council, Melbourne.

Aroviita, J., Hämäläinen, H., (2008). The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes. Hydrobiologia **613**: 45-46.

Badie A, Rondelaud D., (1982). Effect of parasitism on the resistance of *Cionella lubrica* Müller to temperature and desiccation. Ann. Rech. Vet., 13(1):61-7.

Bales, M., Moss, B., Phillips, G., Irvine, K., & Stansfield, J., (1993). The changing ecosystem of a shalloe, brackish lakes, Hickling Broad, Norfolk, U.K.II. Long-term trends in water chemistry and ecology and their implications for restoration of the lake. Freshwater Biology **29**: 141-165.

Bataille, K.J., & Baldassarre, G.A., (1993). Distribution and abundance of aquatic macroinvertebrates following drought in three prairie pothole wetlands. Wetlands, **13** (4): 260 – 269.

Baumgärtner, D., Mörtl, M., Rothhaupt, K.O., (2008). Effects of water-depth and water-level fluctuations on the macroinvertebrate community structure in the littoral zone of Lake Constance. Hydrobiologia **613**: 97-107.

Baumgärtner, D., (2004). Principles of Macroinvertebrate Community Structure in the Littoral Zone of Lake Constance. Verlag Regionalkultur, Heidelberg.

Benson, N.G., & Hudson, P.L., (1975). Effects of a reduced fall drawdown on benthos abundance in Lake Francis Case. Transactions of the American Fisheries Society **104**: 526-528.

Bickel, T.O., & Closs, G.P., (2008). Fish distribution and diet in relation to the invasive macrophyte *Lagarosiphon major* in the littoral zone of Lake Dunstan, New Zealand. Ecology of Freshwater Fish **17**: 10-19.

Biggs, B. J. F., & Malthus, T. J., (1982). Macroinvertebrates associated with various aquatic macrophytes in the backwaters and lakes of the Upper Clutha Valley, New Zealand. New Zealand Journal of Marine and Freshwater Research **16**:81-88.

Blinn, D.W., Shannon, B.J., Stevens, L.E., & Carder, J.P., (1995). Consequences of fluctuating discharge for lotic communities. Journal of North American Benthological Society **14**(2): 233-248.

Boner, T.H., & Wilde, G.R., (2002). Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society **131** (6): 1203-1208.

Brauns, M., Garcia, X. F., & Pusch, M. T., (2008). Potential effects of water-level fluctuations on littoral invertebrates in lowland lakes. Hydrobiologia **613**: 5-12.

Brodersen, K. P., Dall, P. C., & Lindegaard, C., (1998). The fauna in the upper stony littoral of Danish lakes: macroinvertebrates as trophic indicators. Freshwater Biology 39:577 592.

Brooks, J. L. & Dodson, S.I., (1965). Predation, body size, and composition of plankton. Science 150: 28–35.

Burns, N.M., Bryers, G., Bowman, E., (2000). Protocols for monitoring Trophic levels of New Zealand Lakes and Reservoirs. Lakes Consulting. *Prepared for:* Ministry for the Environment, Wellington.

Butcher, G., (2009). Economic values. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 101-110.

Carpenter, S.R., Bolgrien, D., Lathrop, R.C., Stow, C.A., Reed, T., & Wilson, M.A., (1998). Ecological and ecomonic analysis of lake eutrophication by nonpoint pollution. Australian Journal of Ecology **23**:68-79.

Chapman, M. A., & Lewis, M. H., (1976). An Introduction to the Freshwater Crustacea of New Zealand. Collins, Auckland, New Zealand.

Chandra, S., Vander Zanden, M.J., Heyvaert, A.C., Richards, B.C., Allen, B.C., & Goldman, C.R., (2005). The effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers. Limnology and Oceanography **50** (5): 1368-1376.

Christensen, D.L., Herwig, C.B., Schindler, D.E., & Carpenter, S.R., (1996). Impacts of Lakeshore Residential Development on Coarse Woody Debris in North Temperate Ecological Applications, **6** (4): 1143-1149

Chow-Fraser, P., Lougheed, V., Le Thiec, V., Crosbie, B., Simser, L., & Lord, J., (1998). Long-term responce of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. Wetlands Ecology and management **6**: 19-42.

Coops H., Beklioglu, M., & Crisman, T.L., (2003). The role of water-level fluctuations in shallow lake ecosystems-workshop conclusions. Hydrobiologia **506**:23-27.

Corbet, P.S., (1962). A biology of dragonflies. H.F & G Withers LTD, London.

Cott, P.A., Sibley, P.K., Somers, W.M., Lilly, M.R., & Gordon, A.M., (2008). A review of water level fluctuations on aquatic biota with an emphasis on fisheries in ice-covered lakes. Journal of the American Water Resources Association **44** (2): 343-359.

Crumpton, W. J. (1977). Notes on occurrence of Odonata in Canterbury and Westland (New Zealand). New Zealand Entomologist **6**:302-304.

Czachorowski, S. (1993). Distribution of Trichoptera larvae in vertical profile of lakes Polskie Archiwum Hydrobiologii, **40** (2): 139-163.

Davenport, J., (1985). Osmotic control in marine animals. Symposia of the Society for Experimental Biology **39**: 207-244.

Dawn, M. J., (1995). A preliminary investigation of the effects of plant material additions on the aquatic invertebrates in Te Waihora (Lake Ellesmere), Canterbury. University of Canterbury, Christchurch.

Della Bella, V., & Mancini, L., (2009). Freshwater diatom and macroinvertebrate diversity of coastal permanent ponds along a gradient of human impact in a Mediterranean eco-region. Hydrobiologia **634**: 25-41.

de Mendoza, G., & Catalan, J., (2010). Lake macroinvertebrates and the altitudinal environment gradient in the Pyrenees. Hydrobiologia **649** (1): 51-72.

Diehl, S., (1992). Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology **73**:1646-1661.

Donohue, I., Donohue, L.A., Ní Ainím, B, Irvine, K., (2009). Assessment of eutrophication pressures on lakes using littoral invertebrates. Hydrobiologia **633**: 105-122.

Drake, D., Kelly, D., Schallenberg, M., Ponder-Sutton, A., & Enright, M., (2009). Shallow coastal lakes in New Zealand: assessing indicators of ecological integrity and their relationship to broad-scale human pressures. *Prepared for:* Department of Conservation. NIWA Client Report: CHC2009-005.

Dynesius., M & Nilsso, C., (1994). Fragmentation and Flow Regulation of River Systems in the Northern Third the World. Science, New Series **266** (5186): 753-762.

Egertson, C.J., Kopaska, J.A. & Downing, J.A., (2004): A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia* 524: 145-156.

Ellis, A., & Macisaac, H.J., (2009). Salinity tolerance of Great Lakes invaders. Freshwater Biology **54**: 77-89.

Facon, B., Machline, E., & David, P., (2004). Variation in desiccation tolerance in freshwater snails and its consequences for invasion ability. Biological invasions **6**: 283-293.

Fenwick, G., & Image, K., (2002). Effects of Lake Ellesmere and Forsyth openings on the Banks Penisula coastal environment. *Prepared for:*Environment Canterbury by NIWA. NIWA Client Report: CHC2002- 036.

Fernández-Aláez, C., Fernández-Aláez, M., & Bécares, E., (1999). Influence of water level fluctuation on the structure and composition of the macrophyte vegetation in two small temporary lakes in the northwest of spain. Hydrobiologia **415**: 155-162.

Fish, G.R., (1966). An artificially maintained trout population in a Northland lake. New Zealand Journal of Science 9, 200-210.

Fisher, P., & Öhl, U. (2005). Effects of water-level fluctuations on the littoral benthic fish community in lakes: a mesocosm experiment. Behavioural Ecology 16: 741–746.

Fisher, S. G. LaVoy, A. (1972). Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. Journal of the Fisheries Research Board of Canada 29, 1472–1476.

Forsyth, D. J., (1978). Benthic macroinvertebrates in seven New Zealand lakes. New Zealand Journal of Marine and Freshwater Research **12**:41-49.

Francis, T.B. & Schindler, D.E., (2006). Degradation of littoral habitats by residential development: Woody debris in lakes of the Pacific Northwest and Midwest, United States. *Ambio* 35: 274-280.

Frazer, S., & Horrell, G., (2002). Estimates of mean annual low flow for Lake Ellesmere tributaries and streams in the little Rakaia zone. Environment Canterbury. Report No U02-29.

Free, G., Solimini, A.G., Rossaro, B., Marziali, L., Giacchini, R., Paracchini, B., Ghiani, M., Vaccaro, S., Gawlik, B.M., Fresner, R., Santner, G., Schönhuber, M., & Cardoso, A.C., (2009). Modelling lake macroinvertebrate species in the shallow sublittoral: relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. Hydrobiologia **633:** 123-136.

Garn, H.S., Elder, J.F., Robertson, D.M., (2003). Why study lakes? An overview of UGS lake studies in Wisconson. U.S. Geological Survey, Wisconsin District.

Gerbeaux, P., & Ward, J. C., (1991). Factors affecting water clarity in Lake Ellesmere, New Zealand. New Zealand Journal of Marine and Freshwater Research **25**:289-296.

Gill, A.B., (2003). The dynamics of prey choice in fish: the importance of prey size and satiation. Journal of Fish and Biology **63**: 105-116.

Glaz, P.N., Nozais, C., & Arseneault, D., (2009). Macroinvertebrates on coarse woody debris in the littoral zone of a boreal lake. Marine and Freshwater Research **60**: 960-970.

Graynoth, E., & Jellyman, D. J. (2002). Growth, survival, and recruitment of juvenile shortfinned eels (*Anguilla australis*) in a large New Zealand coastal lake. New Zealand Journal of Marine and Freshwater Research **36**:25-37.

Graynoth, E., Bennett, L. C., & Pollard, J. C., (1987): Diet of landlocked sockeye salmon (*Oncorhynchus nerka*) and trout in the Waitaki lakes, New Zealand. New Zealand Journal of Marine and Freshwater Research **20**: 537–549.

Greenwood, M.T., & Wood, P.J., (2003). Effects of seasonal variation in salinity on a populations of Enochrus bicolour Frabricius 1972 (Colepotera: Hydrophilidae) and implications for other beetles of conservation interest.

Grove, P., & Pompei, M., (2009). Vegetation of the lakeshore. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 33 -39.

Häkanson, L., Eklund, J.M., (2010). Relationships between Chlorophyll, salinity, Phosphorus and Nitrogen in Lakes and Marine Areas. Journal of Coastal Research **26** (3): 412-423.

Hamill, K., (2006). Snapshot of lake water quality in New Zealand. Opus International Consultants. Ministry for the Environment project 05/06-0573-L. 64p.

Hamilton, D. P., & Mitchell, S. F. (1997). Wave-induced shear stresses, plant nutrients and chlorophyll in seven shallow lakes. Freshwater Biology **38**:159-168.

Hammer, T.U., & Heseltine, M.J., (1988). Aquatic macrophytes in saline lakes of the Canadian prairies. Hydrobiologia **158**: 101-116.

Hanson, J.M., (1990). Macroinvertebrate size-distribution of two contrasting freshwater macrophyte communities. Freshwater Biology **24**: 481-491.

Hanchet, S., (1999). The effects of koi carp on New Zealand's aquatic ecosystems. *New Zealand Freshwater Fisheries Report*, No. 117. pp. 1-41.

Hart, B., Bailey, P., Edwards, P., Hortle, K., James, K., McMahon, A., Meredith, C., & Swadling, K., (1991). A review of salt sensitivity of Australian freshwater biota. Hydrobiologia **210**: 105-144.

Hayward, S.A., & Ward, J.C., (2009). Water quality in the Ellesmere catchment. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 21 -32.

Hayward, S.A., (2007). Report prepared for the Selwyn Waimakariri Groundwater Allocation Zone Hearing. July 2007, Environment Canterbury, Christchurch.

Hawes, I., & Schwarz, A.M., (1996) Epiphytes from a deep-water characean meadow in an oligotrophic New Zealand lake: Species composition, biomass and photosynthesis Freshwater Biology, **36** (2), pp. 297-313.

Hawes, I., & Ward, J.I., (1996). The factors controlling the growth rate and abundance of phytoplankton in Lake Ellesmere. NIWA, *Prepared for:* Environment Canterbury.

Heinsalu, A., Luup, H., Alliksaar, T., Nõges, P., & Ngões, T., (2008). Water level changes in a large shallow lake as reflected by the plankton: periphyton-ratio of sedimentary diatoms. Hydrobiologia **599**: 23-30.

Hemmingsen, M. A., (1997). The coastal geomorphology of Te Waihora. University of Canterbury, Christchurch.

Henrikson, B.I., (1988). The absence of antipredator behaviour in the larvae of *Leucorrhinis dubia* (Odonata) and the consequences for their distribution. Oikos **51**: 170-183,

Hofmann. H., Lorke., & Peeters. F., (2008) Temporal scales of water-level fluctuations in lakes and their ecological implications. Hydrobiologia **613**: 85-96.

Horrell, G., (2008). Lake Ellesmere (Te Waihora) seawater inflows: June-July 2008. NIWA. *Prepared for:* Environment Canterbury, CHC2008-131.

Hudon, C., (1997). Impact of water level fluctuations on St. Lawrence River aquatic vegetation. Canadian Journal of Fisheries and Aquatic Sciences 54: 2853–2865

Hughes, H. R., McColl R. H. S., & Rawlence D. J. (1974). Lake Ellesmere, Canterbury, New Zealand: A review of the lake and its catchment. N.Z. Dept. of Scientific and Industrial Research, Information series.

Hughey, F.D., & Taylor, K.J.W., (2009). Te Waihora/Lake Ellesmere State of the lake and future management. EOS Ecology ISBN 978-0-473-1496-1.

Hughey, F.D., & O'Donnell., C.F.J., (2009). Birdlife of the lake. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 57 -75.

Hughey, F.D., Taylor, K., & Ward, J.C., (2009). Current state and future management. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 112-131.

Hunt, P.C., & Jones, J.W., (1972). The effect of water level fluctuations on a littoral fauna. Journal of Fish Biology 4, 385–394.

Jack, J.D., Wickham, S.A., Toalson, S., & Gilbert, J.J., (1993). The effect of clays on a freshwater plankton community: An enclosure experiment Archiv für Hydrobiologie **127**: 257-270.

James, K.R., Cant. B., & Ryan, T., (2003). Responses of freshwater biota to rising salinity level and implications for saline water management: a review. Australian Journal of Botany **51**: 703-713.

James, G.D., & Graynoth, E. (2002). Influence of fluctuating lake levels and water clarity on trout populations in littoral zones of New Zealand alpine lakes. New Zealand Journal of Marine and Freshwater Research **36**: 39-52.

James, M. R., Hawes, I., Weatherhead, M., Stanger, C. & Gibbs, M,. (2000). Carbon flow in the littoral food web of an oligotrophic lake. Hydrobiologia **441**:93-106.

James, M. R., Weatherhead, M., Stanger, C. & Graynoth, E., (1998). Macroinvertebrate distribution in the littoral zone of Lake Coleridge, South Island, New Zealand – effects of habitat stability, wind exposure, and macrophytes. New Zealand Journal of Marine and Freshwater Research **32**:287-305.

Jellyman, D., & Smith, C., (2009). Native fish and fisheries. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 42-48.

Jellyman, D., Walsh, J., de Winton, M., & Sutherland, D., (2009). A review of the potential to re-establish macrophyte beds in Te Waihora (Lake Ellesmere). NIWA. *Prepared for:* Environment Canterbury, CHC2008-142.

Jellyman, D. J., & Chisnall, B. L., (1999). Habitat preferences of shortfinned eels (*Anguilla australis*), in two New Zealand lowland lakes. New Zealand Journal of Marine and Freshwater Research **33**:233-248.

Jellyman, D. J., & Todd, P. R., (1998). Why are migrating male shortfinned eels (*Anguilla australis*) in Lake Ellesmere, New Zealand, getting smaller but not younger? Bulletin Francais de Pêche at Pisciculture **349**:141-152.

Jeppesen, E., Søndergaard, M., Pedersen, A.R., Jürgens, K., Strzelczak, A., Lauridsen, T.L., & Johansson, L.S., (2007). Salinity induced regime shift in shallow brackish lagoons. Ecosystems **10**: 47-57.

Jeppesen, E., Søndergaard, M., Jensen, J.P., Kanstrup, E., & Pedersen, L.J., (1997). Macrophytes and turbidity in brackish lakes, with special emphasis on the role top down control. *In*: Jeppesen, E., Søndergaard, M., & Kristoffersen, K (eds) The structuring role of submerged macrophytes in lakes,

Jeppesen, E., Søndergaard, M., Kanstrup, E., Pedersen, A.R., Henriksen, R.B., Hammershøj, M., Mortensen, E., Jensen, J.P., & Have, A., (1994). Does the impacts of nutrients on the biological structure and function of brackish and freshwater lakes differ? Hydrobiologia **275/276**: 15-30.

Jensen, J.P., Kristensen, P., & Jeppesen, E., (1991). Relationships between N loading and in lake N concentrations in shallow Danish lakes. **24**: 201-204.

Johansson, F., Englund, G., Brodin, T., & Gardfjell, H., (2006). Species abundance models and patterns in dragonfly communities: effects of fish predators. Oikos **114**: 27-36.

Johnson, R.K., & Goedkoop, W., (2002). Littoral macroinvertebrate communities: spatial scale and ecological relationships. Freshwater Biology **47**: 1840-1854.

Johnson, P. N., & Partridge, T.R., (1998). Vegetation and water level regime at Waituna Lagoon, Southland. Department of Conservation, Wellington.

Johnson, D.M., (1991). Behavioural ecology of larval dragonflies and damselflies. Trends in Ecology and Evolution **6**: 8-13.

Juutinen, S., Alm, J., Martikaninen, P., & Silvola, J., (2001). Effects of spring flood and water level draw-down on methane dynamics in the littoral zone of boreal lakes. Freshwater Biology **45**: 855-869

Kadoya, T., Suda, S. & Washitani, I., (2004). Dragonfly species richness on man-made ponds: Effects on ponds size and pond age on newly established assemblages. Ecological Research **19**:461-467.

Kefford, B.J., Zalizniak, L., & Nugegoda, D., (2006). Growth of the damselfly *Ischnura heterosticta* is better in saline water than freshwater. Environmental Pollution **141**: 409-419.

Kefford, B.J., Papas, P.J., Metzeling, L., & Nugegoda, D., (2004). Do laboratory salinity tolerances of freshwater animals correspond with their field salinity? Environmental Pollution **129**: 355-362.

Kefford, B.J., Papas, P.J., & Nugegoda, D., (2003). Relative salinity tolerance of macroinvertebrates from the Barwon River, Vitoria , Australia. Marine and Freshwater Research European Journal of Wildlife Reserve **54**: 755-765.

Kelly, D., & Jellyman, D., (2007). Changes in trophic linkages to shortfin eels (*Anguilla australis*) since the collapse of submerged macrophytes in Lake Ellesmere, New Zealand. *Hydrobiologia* **579:** 161-173.

Kelly, D., & Hawes, I. (2005). Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high country lake. Journal of the North American Benthological Society **24** (2): 300-320.

Kelly, D., & McDowall, R., (2004). Littoral invertebrate and fish communities *In*: Freshwater of New Zealand. Chapter 25: 25.1-25.14.

Keast, A., & Harker, J., (1977). Fish distribution and benthic invertebrate biomass relative to depth in an Ontario lake. Environmental Biology of Fishes **2** (3): 235-240.

Keto, A., Tarvanien, A., Marttunen, M., & Hellsten, S., (2008). Use of the water-level fluctuation analysis tool (Regcel) in hydrological status assessment of Finish lakes. Hydrobiologia **613**: 113-142.

Kirk, R. M., & Lauder, G. A. (2000). Significant coastal lagoon systems in the South Island, New Zealand - Coastal processes and lagoon mouth closure. Science for Conservation **146**:47 pp.

Kirk, R. M., (1994). The origins of Waihora/Lake Ellesmere. Pages 9-16 *in* J. D. G. Davies, Galloway, L. & Nutt, A. H. C., editor. Waihora Lake Ellesmere, past present future, Lincoln.

Kirk, R.M., & Henriques, P.R., (1986). Physical and biological aspects of shoreline change: Lake Ohau, South Island. New Zealand Journal of Shoreline Management **2**: 305-326.

Kornijo´w, R., (1988). Distribution of zoobenthos in littoral of two lakes differing in trophy. Polskie Archiwum Hydrobiologii 35: 185–195.

Larned, S., & Schallenberg, M., (2006). Constraints on phytoplankton production in Lake Ellesmere. *Prepared for:* Environment Canterbury. NIWA Client Report: CHC2006-101.

Leira, M., & Cantonati, M., (2008). Effects of water-level fluctuations on lakes: an annotated bibliography. Hydrobiologia **613**: 171-184.

Lepš, J., & Šmilauer, P., (2003). Multivariate Analysis of Ecological Data using CANOCO. Cambrige University Press.

McAfee, M. E., (1980). Effects of water drawdown on the fauna in small cold water reservoirs. Water Resources Bulletin **16**: 690–696.

McDowall, R. M., (1968). Interactions of the native and alien faunas of New Zealand and the problem of fish introductions. Transactions of the America Fisheries Society 97: 1-11.

McGowan, S., Leavitt, P.R., & Hall, R.I., (2005). A whole-lake experiment to determine the effects of winter droughts on shallow lakes. Ecosystems **8**: 694–708.

McEwen, D.C., & Butler, M.G., (2010). The effects of water-level manipulation on the benthic invertebrates of a managed reservoir. Freshwater Biology **55**: 1086-1101.

McPeek, M.A., (1990). Behavioural differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. Ecology **71**: 1712-1726.

Moore, N.W (1989). A visitor's observations on the dragonfly's of New Zealand and their conservation. New Zealand Entomologist Vol 12: 5 -13.

Moore, J.W., (2006). Animal ecosystem engineers in streams. BioScience **56**: 237-246.

Moss, B., (1994). Brackish and freshwater shallow lakes - different systems or variations on the same theme? Hydrobiologia **275/276**: 1-14.

Mörtl, M., (2003): Biotic interactions in the infralittoral of Lake Constance. – Dissertation thesis, University Konstanz, pp.163 .

Næstad, F., & Brittain, J.E., (2010). Long-term changes in the littoral benthos of a Norwegian subalpine lake following the introduction of the European minnow (Phoxinus phoxinus). Hydrobiologia **642**: 71-79.

Nurminen. L., Pekcan-Hekim. Z., Repka, S., & Horppila, J., (2010). Effect of prey type and inorganic turbidity on littoral mpredator–prey interactions in a shallow lake: an experimental approach. Hydrobiologia **646**: 209-214.

Oberholster, P.J., Botha, A.M., & Ashton, P.J., (2009). The influence of toxic cyanobacterial bloom and water hydrology on algal populations and macroinvertebrate abundance in the upper littoral zone of Lake Krugersdrift, South Africa. Ecotoxicology **18**: 34-46.

O'Donnell, H., (1989). Habitat use by waders and waterfowl at Lake Ellesmere in relation to water level fluctuations. Department of Conservation.

Oscarson, H.G., (1987). Habitat segregation in a water boatmen (Corixidae) assemblage – the role of predation. Oikos **49**: 133-140.

Palomaki, R., (1994): Response by macrozoobenthos biomass to water-level regulation in some Finnish lake littoral zones. Hydrobiologia **286**: 17-26.

Parsons, B.G., Watmough, S.A., Dillion, P.J., & Somers, K.M. (2010). Relationships between lake water chemistry and benthic macroinvertebrates in the Athabasca Oil Sands Region, Alberta. Journal of Limnology **69**: 118-125.

Pearsall, W.H., (1920) The aquatic vegetation of the English lakes. J Ecology **8**: 164-201.

Piscart, C., Moreteau, J.C., & Beisel, J.N. (2006). Monitoring changes in freshwater macroinvertebrate communities along a salinity gradient using artificial substrates. Environmental Monitoring and Assessment **116**: 529-542.

Pompei, M., & Grove, P., (2009). Distribution and abundance of introduced willows in Lake Ellesmere/Te Waihora shoreline wetlands. Environment Canterbury. Report No. R09/25.

Prus, T., Prus, M. Bijok, P. (1999). Diversity of invertebrate fauna in littoral of shallow Myczkowce dam reservoir in comparison with a deep Solina dam reservoir. Hydrobiologia 408/409, 203–210.

Qin, B., Liu, Z., & Haven, K., (2007) Eutrophication of shallow lakes with special reference to Lake Taihu, China. Hydrobiologia **581** (194).

Quinn, G.P., & Keough, M.J., (2002). Experimental design and data analysis for biologists. Cambridge University Press. Chapter 4: 58-71.

Reid, M., (2005). Diatom-based models for reconstructing past water quality and productivity in New Zealand lakes. Journal of Paleolimnology **33**: 13-38.

Remane, A., (1934). Die Brackwasserfauna. Varhandlungen der Deutschen Zollogischen Gschellschaft **36**: 34-74.

Remsburg, A.J., & Turner, M.G., (2009). Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. Journal of the North American Benthological Society **28** (1): 44-56.

Richardson, S. M., Hanson, J. M., & Locke, A., (2002). Effects of impoundment and water-level fluctuation on macrophyte and macroinvertebrate communities of a dammed tidal river. Aquatic Ecology 36, 493–510.

Romano, M., Barberis, I., Pagano, F., & Maidagan, J., (2005). Seasonal and interannual variation in waterbird abundance and species composition in the Melincué saline lake, Argentina. European Journal of Wildlife Research **51**: 1-13.

Rørslett, B., (1989). An integrated approach to hydropower impact assesment. II. Submerged macrophytes in some Norwegian hydro-electric lakes. Hydrobiologia 175:65-82.

Rørslett, B., (1984). Environmental factors and aquatic macrophyte response in regulated lakes - a statistical approach. Aquatic Biology **19** (3-4): 199-220.

Rowe, D. K., Konui. G., & Christie. K. D., (2003). Population structure, distribution, reproduction, diet, and relative abundance of koaro (*Galaxias brevipinnis*) in a New Zealand lake. Journal of the Royal Society of New Zealand. **32** (2): 275-291.

Reynoldson, T.B., Norris, R.H., Resh, V.H., Day, K.E. & Rosenberg, D.M., (1997): The reference condition: A comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J. N. Am. Benthol. Soc.* 16: 833-852.

Ryan, P.A., (1986). Seasonal and size-related changes in the food of the short-finned eel, Anguilla autralis in Lake Ellesmere, Canterbury, New Zealand. Environmental Biology of Fishes **15**: 47–58.

Sagar, P.M., Hawes, I., Stephens, S., Jellyman, D., & Kelly, D., (2004). Lake Ellesmere (Te Waihora): a review of water clarity and the potential for macrophyte growth, and benthic invertebrates, fisheries and birds, and their feeding relationships. NIWA. *Prepared for:* Environment Canterbury, CHC2004-068.

Sagar, P.M., Schwarz, A.M., & Howard-Williams, C., (1995). Review of the ecological rols of Black Swan (*Cygnus atratus*). NIWA No.25.

Sanders, M. D. 1996: Effects of fluctuating lake levels and habitat enhancement on black stilts *(Himantopus novaezelandia).* Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand.

Sanders, M.D., & Maloney, R.F. (1994). Enhancements of invertebrate food supplies for Black Stilts by manipulating wetland and stream substrata. pp 7- 18 *in* Collier, K.J. (Ed), Restoration of Aquatic Habitats.

Savage, A.A. (1982). Use of water boatmen (Corixidae) in the classification of lakes. Biological Conservation **23**: 55-70.

Scarsbrook, M.R & McBride, G.B. 2007. Best practice guidleines for the statistical anlysis of freshwater quality data (Version 1). *Prepared for:* Ministry for the Environment. NIWA Client Report: HAM2007-088. pg 18-19.

Schallenberg, M., Larned, S.T, Hayward, S., & Arbuckle, C., (2010). Contrasting effects of managed opening regimes on water quality in two intermittently closed and open coastal lakes. Estuarine, Coastal and Shelf Science x x x 1 -11pp.

Schallenberg, M. & Burns, C.W., (2004). Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. Freshwater Biology **49**: 143-159.

Schallenberg, M., & Waite, E., (2004). Survey of aquatic macrophytes in Lake Waihola Summer 2002-2003. Limnology Report No. 9. Department of Zoology, University of Otago, Dunedin.

Schallenberg M. & Burns C.W., (2003) A temperate, tidal lake-wetland complex 2. Water quality and implications for zooplankton community structure. *New Zealand Journal of Marine and Freshwater Research* **37**: 429-447

Scheffer, M., & van Nes. E.H., (2007). Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia **584**: 455-466.

Scheffer, M., (2001). Ecology of Shallow Lakes. Chapman & Hall, London.

Scheifhacken, N., Fiek, C., Rothhaupt, K., (2007). Complex spatial and temporal patterns of littoral benthic communities interacting with water level fluctuations and wind exposure in the littoral zone of a large lake. Fundamental and Applied Limnology **169** (2):115-129.

Segal S (1971) Principles on structure, zonation and succession of aquatic macrophytes. Hidrobiologia **12**:89-95.

Sih,A., (1982). Foraging Strategies and the Avoidance of Predation by an Aquatic Insect, Notonecta Hoffmanni. Ecology **63** (3): 786-796.

Søndergaard, M., Jeppesen, E., Lauridsen, T.L., Skov, C., Van Nes, E.H., Roijackers, R., Lammens, E. & Portielje, R. (2007) Lake restoration: successes, failures and long-term effects. *Journal of Applied Ecology*, **44**, 1095–1105.

Spigel, B., (2009). Salinity balance model for Lake Ellesmere/Te Waihora and results from salinity-temperature surveys. *Prepared for:* Environment Canterbury. NIWA Client Report:CHC2009-174.

Smith, B. D., Maitland. P. S., & Pennock. S.M., (1987). A comparative study of water level regimes and littoral benthic communities in Scottish Lochs. Biological Conservation 39: 291–316.

Stark, J.D., (1981). Trophic interrelationships, life histories and taxonomy of some invertebrates associated with aquatic macrophytes in Lake Grassmere. Department of Zoology, University of Canterbury.

Strayer, D. L., Lutz, C., Malcom, H.M., & Munger, K., (2003). Invertebrate communities associated with a native (*Vallisneria Americana*) and an alien (*Trapa natans*) macrophyte in a large river. Freshwater Biology **48**: 1938-1949.

Sutela, T., & Vehanen, T., (2008). Effects of water-level regulation on the nearshore fish community in boreal lakes. Hydrobiologia **613**: 13-20.

Swanson, G.A., & Meyer, M.I., (1977). Impact of fluctuating water levels on feeding ecology of breeding Blue-Winged Teal. The Journal of Wildlife Management **41**(3): 426-433.

Talbot, J. M., & Ward, J. C., (1987). Macroinvertebrates associated with aquatic macrophytes in Lake Alexandrina, New Zealand. New Zealand Journal of Marine and Freshwater Research **21**:199-213.

Takamura, N., Ito, T., Ueno, R., Ohtaka, A., Wakana, I., Nekagawa, M., Ueno, Y., & Nakajima, H., (2009). Environmental gradients determining the distribution of benthic macroinvertebrates in Lake Takkobu, Kushiro wetland, northern Japan. Ecological Research **24**: 371-381.

Taylor, K. J. W., (Ed). (1996). The Natural Resources of Lake Ellesmere (Te Waihora) and its Catchment. Canterbury Regional Council Report R96 (7), Christchurch.

Te Runanga o Ngai Tahu, D. o. C. (2005). Te Waihora Joint Management Plan. Christchurch, New Zealand.

Thompson, R. M., & Ryder, G. R., (2008). Effects of hydro-electrically induced water level fluctuations on benthic communities in Lake Hawea, New Zealand. New Zealand Journal of Marine and Freshwater Research **42**: 197-206.

Thompson, R. M., & Ryder, G. R., (2003). Waituna lagoon: summary of existing knowledge and identification of knowledge gaps. Science for Conservation **215**:37 pp.

Thorp, J.H., Covich, A.P., (1991). Freshwater invertebrates; Ecology; Classification; North America. Academic Press, San Diego ISBN 0126906459.

Timmermans, S.TA., Badzinski, S.S & Ingram, J.W., (2008). Associations between Breeding Marsh Bird Abundances and Great Lakes Hydrology. Journal of Great Lakes Research. 32 (2) 351-364.

Timms, B. V., (1982). A study of the benthic communities of twenty lakes in the South Island, New Zealand. Freshwater Biology **12**:123-138.

Timms, B. V., (1983). Benthic macroinvertebrates of seven lakes near Cass, Canterbury high country, New Zealand. New Zealand Journal of Marine and Freshwater Research **17**:37-49.

Tolonen, K. T., H. Hamalainen, I. J. Holopainen & J. Karjalainen., (2001). Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. Archiv für Hydrobiologie **152**: 39–67.

Traut, A.H., & Hostetler, M.E., (2003) Urban Lakes and Waterbirds: Effects of Development on Avian Behavior. The International Journal of Waterbird Biology **26** (3): 290-302.

Trotzky, H.M., & Gregory, R.W., (1974). The effects of water flow manipulation below a hydroelectric power dam on the bottom fauna of the upper Kennebec River, Maine. Transactions of the American Fisheries Society **103**: 318–324.

Turner, M.G., Huebert, D.B., Findlay, D.L., Hendzel, L.L., Jansen, W.A., Bodaly, R.A., Armstrong, L.M., & Kasian, S.E.M., (2005). Divergent impact of experimental lake level drawn-down on planktonic and benthic plant communities in a boreal forest lake. Canadian Journal of Fisheries and Aquatic Sciences **62** (5): 991-1003.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup , H.H., Christoffersen , K., & Lodge, D.M., (2003). From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnology and Oceanography **48**(4): 1408-1418

Van de Meutter, F., De Meester, L. & Stoks, R., (2005). Water turbidity affects predator-prey interactions in a fish-damselfly system. Behavioural Ecology **144**:327-336.

Vant, W.N., (1987). Lake managers handbook: A guide to understanding investigations into lake ecosystems, so as to assess management options for lakes. Water and Soil Miscellaneous Publications No. 103, pp 12.

Verschuren, D., Tibby, J., Sabbe, K., Roberts, N., (2000). Effects of depth, salinity and substrate on the invertebrate community of fluctuating tropical lake. Ecology **81** (1): 164-182.

Wantzen, K. M., Rothhaupt, K., Mörtl, M., Cantonati, M., Tóth, L.G., & Fischer, P., (2008). Ecological effects of water-level fluctuations in lakes: an urgent issue. Hydrobiologia **613**: 1-4.

Ward, J.C., Fietje, L., Freeman, M.C., Hawes, I., & Smith, V.R., (1997). *In:* Taylor, K..J.W., (eds). The Natural Resources of Lake Ellesmere (Te Waihora) and its catchment. Environment Canterbury. Report 96(7). ISBN 1-86937-262-x. Chapter 8 pg 116.

Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., & Brendonck, L., (2008). Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. Freshwater Biology **53**: 1808-1822.

Weatherhead, M. A., & James, M. R., (2001). Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. Hydrobiologia **462**:115-129.

Wellborn, G.A., Shelly, D.K., & Werner, E.E., (1996). Mechanisms creating community structure across a freshwater habitat gradient. Annual review of Ecology and Systematics **27**: 333-367.

Wetzel, R.G., (2001). Fundamental processes within natural and constructed wetland ecosystems: Short-term versus long-term objectives. Water Science and Technology **44** (11-12): 1-8.

Wetzel, R.G., (1983). Limnology, Second Edition. Saunders College Publicating, Philadelphia.

White, M.S., Xenopoulos, M.A., Hogsden, K., Metcalfe, R.A., Dillon, P.J. (2008). Natural lake level fluctuation and aquatic communities within small lakes of the Laurentian Great Lakes region. Hydrobiologia **613**: 21-31.

Whitfield, C.J., Aherne, J., Cosby, B.J., Watmough, S.A., (2010) Modelling boreal lake catchment response to anthropogenic acid deposition. *Journal of Limnology* **69** (SUPPL 1) pp 135-146.

Williams, H., (2009). Groundwater and the 'living lake'. *In*: Hughey, K.F.D. and Taylor, K.J.W. (eds.). *Te Waihora/Lake Ellesmere: State of the lakes and future management.* EOS Ecology, Christchurch, Pp 10 -19.

Williams, W.D. (1999). Salinisation: A major threat to water resources in the arid and semi-arid regions of the world. Lakes and Reservoirs: Research and Management **4**: 85-91.

Williams, W. D., Boulton, A. J. & Taaffe, R. G. (1990). Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia **197**:257-266.

Williams, D.D., & Williams, N.E., (1998). Aquatic insects in an estuarine environment: densities, distribution and salinity tolerance. Freshwater Biology.

Winterbourn, M. J., Gregson, K. L. D. & Dolphin, C. H., (2000). Guide to the aquatic insects of New Zealand. 3rd Edition, Auckland, New Zealand.

Winterbourn, M.J., & Lewis, M.H., (1975). Littoral fauna. *In*: Jolly, Z.H., & Brown, J.M.H. (eds), New Zealand lakes. Auckland University Press/Oxford University Press, Auckland, 271-280.

Winterbourn, M.J., (1970): Population studies on the New Zealand freshwater gastropod *Potamopyrgus antipodarum* (Gray). Proceedings of the Malacological Society, London 39: 139-149.

Wissinger, S.A., Greig, H., & McIntosh, A., (2009) Absence of species replacements between permanent and temporary lentic communities in New Zealand. Journal of the North American Benthological Society **28**(1):12–23.

Wissinger, S.A., McIntosh, A., & Greig, H., (2009-2028). Impacts of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zealand lakes. Freshwater Biology **51**.

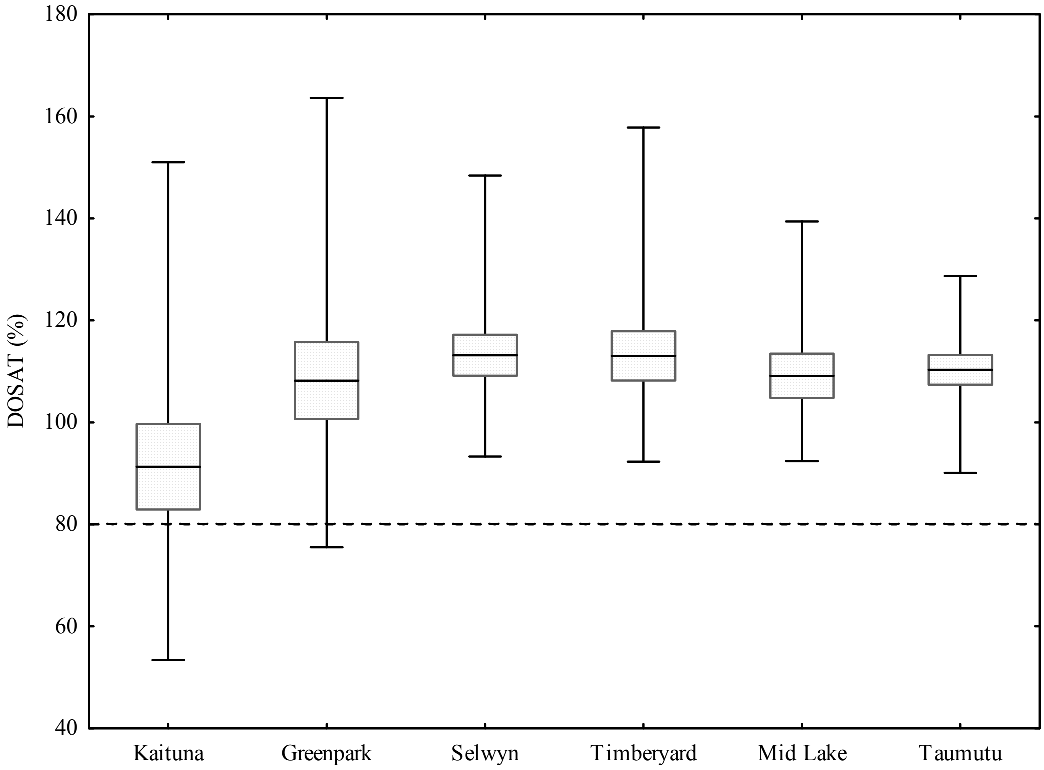
Wittwer, T., Sahlén, G., & Suhling, F., (2010). Does one community shape the other? Dragonflies and fish in Swedish lakes. Insect Conservation and Diversity **3**: 124-133.

Wollheim, W.M., & Lovvorn, J.R., (1995). Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming High Plains. Hydrobiologia **310**: 207-223.

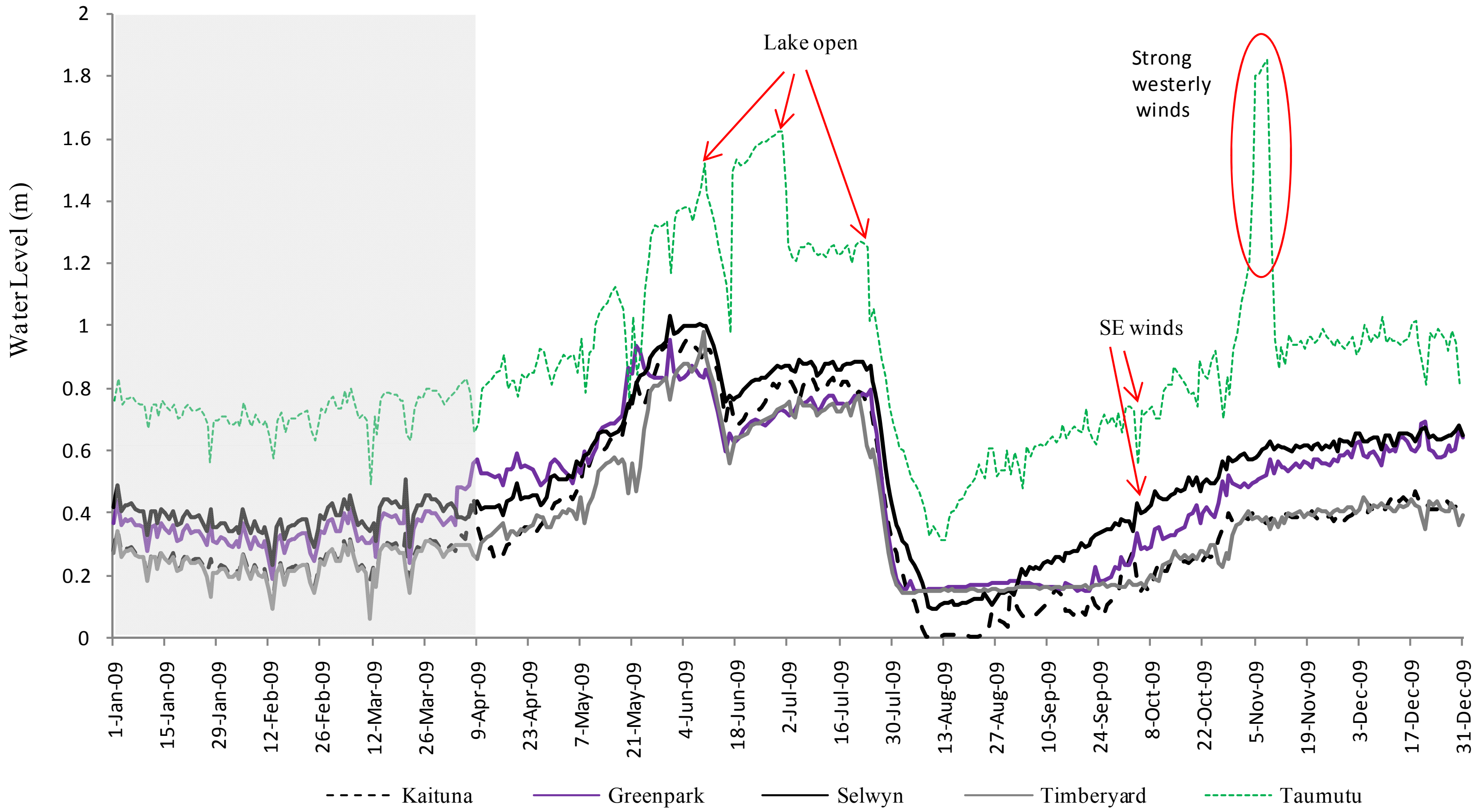
Wood, H., (2008). *Thesis:* The benthic ecology and food wed of Te Waihora (Lake Ellesmere). University of Canterbury.

Yeates, G. W., (1965). The benthos of Lake Ellesmere. University of Canterbury, Christchurch.

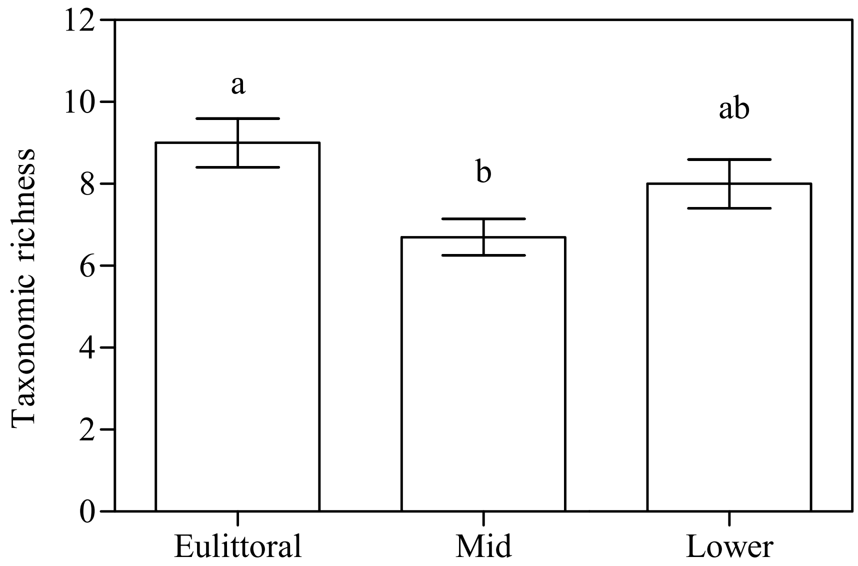
Appendix 1 Spot dissolved oxygen saturations at five sites around Lake Ellesmere/Te Waihora January – December 2009.



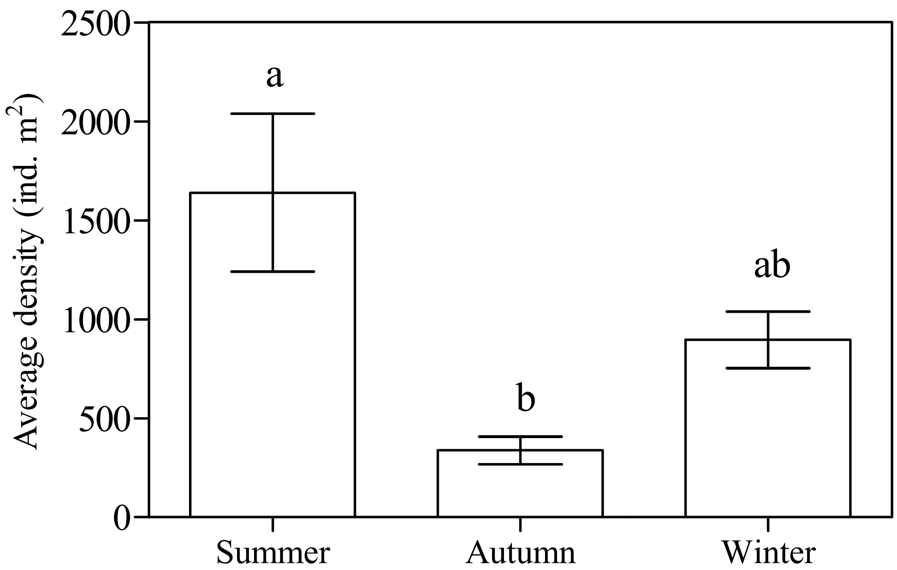
Appendix 2 Water level at five sites around Lake Ellesmere/Te Waihora January – December 2009. Grey block indicates estimated water levels.



Appendix 3 Invertebrate communities in three season in Lake Ellesmere/Te Waihora A) Taxonomic richness in the littoral zone. B) Average density in the eulittoral zone. (Mean ± 1SE).



A



B

Appendix 4 Results of Analysis of Similarities (ANOSIM) on invertebrate composition data for five sites around Lake Ellesmere/Te Waihora 2009.

ANOSIM		R -statistic	*p* value
Littoral zone		0.039	0.22
	Eulittoral vs Mid	0.038	0.252
	Eulittoral vs Lower	**0.149**	**0.054**
	Mid vs Lower	-0.068	0.832
Spatial		0.192	0.002
	Kaituna vs Greenpark	**0.31**	**0.02**
	Kaituna vs Selwyn	**0.259**	**0.041**
	Kaituna vs Timberyard	-0.009	0.479
	Kaituna vs Taumutu	**0.368**	**0.023**
	Greenpark vs Selwyn	0.019	0.305
	Greenpark vs Timberyard	0.037	0.284
	Greenpark vs Taumutu	**0.571**	**0.002**
	Selwyn vs Timberyard	0.055	0.207
	Selwyn vsTaumutu	**0.288**	**0.037**
	Timberyard vs Taumutu	**0.39**	**0.006**
Seasonal			
Summer vs Winter		**0.117**	**0.02**
Eulittoral		**0.232**	**0.037**
	Summer vs Autumn	0.188	0.143
	Summer vs Winter	**0.312**	**0.079**
	Autumn vs Winter	0.163	0.198